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Effects of insect herbivory in herbaceous communities: coarse and fine-scale examination

by

Malcolm Douglas Coupe



A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the
requirements for the degree of Master of Science

in

Environmental Biology and Ecology

Department of Biological Sciences

Edmonton, Alberta

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(Committee member)

September 30th 2003
Date

ABSTRACT

I examine the effects of insect herbivory on plant communities, and the properties of plant communities that regulate those effects, with an emphasis on the role of insect herbivory in rough fescue prairie. I begin with a meta-analysis of studies that have chemically suppressed insects in herbaceous plant communities, and measured its effect on primary production. Effect size did not depend upon productivity or plant species richness, but did depend upon community type. Next I examine the consequences of insect suppression in the rough fescue prairie of Kinsella Ranch, Alberta, in the aspen parkland ecoregion. Insects did not alter primary production or focal plant performance, but in the second year of the study (and of a drought), insects reduced canopy cover and species richness. I conclude that insect herbivory affects community structure, at least under drought conditions. Lastly, I show that the soil insect herbivores at this site were at low densities unlikely to have affected plant growth.

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LIST OF ABBREVIATIONS

AGI	Above-ground insecticide
BGI	Below-ground insecticide
C.I.	Confidence interval
Den df	Denominator degrees of freedom
GLIMMIX	Generalized linear mixed model
MRBP	Blocked Multiple Response Permutation Procedure
Num df	Numerator degrees of freedom
NS	Not significant
P	Probability of the resulting test statistic if H_0 is true
x	Interaction (e.g. "AGI x BGI")

CHAPTER 1

GENERAL INTRODUCTION

Herbivory may play a minor role in plant community dynamics of natural ecosystems, either because herbivore populations are maintained at low levels by their predators (Hairston et al., 1961; Strong et al., 1984; Marquis and Whelan, 1994), plants present nutritional and physical impediments to the herbivores that would convert them to their own tissue (McNeil and Southwood, 1978; Price, 1992; Awmack and Leather, 2002), or some combination of, or interaction between, these factors (Janzen, 1988; Power, 1992; Coley and Barone, 1996). Referring to invertebrates in particular, Crawley (1989) argued that invertebrate herbivores are less important to plant population dynamics than are vertebrates, due to their lower body size and metabolic rate, greater food specificity, and lower starvation tolerance. This theoretical framework leaves little room for an important role of insect herbivory in plant community structure.

One prediction of this body of theory is that long-term removal of insects from a herbaceous community will have minor impact on focal plant performance or plant community structure. Crawley (1989) reviewed a number of long-term studies that had used (or were using) this method, and concluded that insect herbivory sometimes has strong effects on individual plant performance, but that the existing evidence supported his view that insects are largely unimportant to primary production and plant population dynamics. Not all of these studies were complete at the time of his review, and they eventually provided mixed support

for his predictions, with some studies showing little or no effect of insect removal on plant community structure or primary production (Crawley, unpublished; Gibson et al., 1990) while others have demonstrated dramatic effects on succession, primary production, and plant population dynamics (Brown and Gange, 1992; Carson and Root, 2000).

The authors that had found these strong effects argued that previous research had not given consideration to the full suite of insect herbivores present in herbaceous communities. Specifically, Brown and Gange (1992) concluded that below-ground insect herbivory can have strong effects on plant community composition during early secondary succession. They argued that by considering only foliar feeders, previous workers had underestimated the effects of insect herbivores on succession. Carson and Root (2000) examined long-term effects of an outbreaking specialist insect herbivore on old field succession, and concluded that outbreaks have persistent effects on community structure that extend beyond their duration.

The use of insects for the biological control of weeds has shown that specialist insect herbivores outside their native range can have dramatic effects on the performance of their plant host (Wu et al., 1999; Center et al., 1999; Dhileepan et al., 2000). These may have cascading effects on the plant community as a whole (Huffaker and Kennett, 1959; de Bach, 1991). Such effects run contrary to the general assumption that insect herbivores are not important to plant community structure, but they can actually be seen as evidence for top-down effects of the natural enemies of insect herbivores; the

specialist insect herbivores may have such effects only because they are released from the suite of predators found in their native habitat (de Bach, 1991).

This debate continues, with an accumulation of evidence for top-down control of insect herbivore populations (Schmitz et al., 2000), forceful arguments for the hypothesis that insect herbivores encounter a poverty of food despite an apparent plenty (Hartley and Jones, 1997), and further evidence for insect herbivores playing a strong role in affecting community structure (Bach, 1994; Schädler et al., unpublished). This literature has developed to the point where a number of questions can be addressed: 1) Given that insects strongly affect community structure in some systems, yet not in others, can any general conclusions be reached regarding the properties of the system that modulate these impacts? 2) Are there systems (communities or herbivore types) where effects of insect herbivory have not been measured? 3) What can we infer from measurement of insect herbivore impacts in these systems?

The goal of this thesis is to address these questions by examining effects of experimental manipulation of insect numbers on herbaceous plant communities. In such designs, insecticides are used to reduce insect numbers in a grassland or forb-dominated community, and various measures of plant community response are taken as suppression continues (Clements et al., 1982; Brown and Gange, 1992). Conclusions regarding the effects of insects on community structure or function are drawn from the results.

In Chapter 2, I examine studies that have used this design to measure effects of insects on primary production, measured as standing biomass. I create a

database consisting of the results from each study, and test hypotheses for the conditions under which insects have the greatest potential to reduce primary production, using the statistical technique of meta-analysis (Gurevitch and Hedges, 1999). Of greatest interest is to extend the exploitation ecosystems hypothesis of Oksanen et al. (1981) to insects. Specifically, I wish to determine whether productivity modulates the relative strengths of top-down and bottom-up forces, as they might determine the impact of insect herbivory. Another goal is to examine Root's (1973) theories regarding the effect of plant diversity on insect herbivore density, as it might apply to natural communities, rather than the agricultural communities for which it had been developed. I wish to determine whether more diverse plant communities have proportionately less biomass removed by insects, as is expected if more diverse communities make food less accessible to insect herbivores, or allow their natural enemies to operate with greater efficiency. I search for further sources of variation in the data by determining whether response to insect suppression is dependent upon outbreak status or plant species composition.

Insect herbivory may radically change the species composition and diversity of a plant community while having little effect on gross measures of community structure such as total cover (Huffaker and Kennett, 1959), and biomass (Gibson et al., 1990). As such, any observation of negligible effects on such aggregate measures may not detect an important role for insect herbivory in plant community dynamics. Chapter 3 describes a two year experiment in which above- and below-ground insects were suppressed in native grassland whose

above-ground insect fauna is numerically dominated by herbivores. Several traits of the whole plant community and individual plant growth are measured. I test the following hypotheses: 1) insects alter primary production and root biomass, 2) insects affect vegetative cover and plant species richness, 3) insects affect performance of the dominant plant species, with negative effects on species that experience more insect herbivory, and 4) plant community composition is altered by insects.

Although the effects of above-ground insects on plant community structure are becoming increasingly apparent, it is generally agreed that the effects of soil arthropods on plant growth remain poorly understood (Mortimer et al., 1998, Blossey and Hunt-Joshi 2003). In Chapter 4, I address this topic with a survey of the taxonomic composition and density of the dominant soil arthropods of a native grassland site, especially the macroarthropods. With reference to the literature, the feeding habits of the dominant taxa are established, as well as the densities at which they are thought to have had a substantial impact on plant community structure in other graminoid communities. I also evaluate the effectiveness of the above- and below-ground insecticide treatments in controlling soil arthropods. That chemical manipulation has been effective is a critical assumption of these types of studies, and one, which is often not evaluated, or at least reported (e.g. Brown and Gange 1989, 1992).

Thesis objectives

My overall objective is to examine how insect herbivory affects the basic measures by which plant communities are described. I begin with a coarse-scale examination of the average effect of insects on primary production, and of the properties of the plant community that mediate that effect. I then describe a two-year experiment in which I manipulated insect herbivore numbers and measured their impact on several measures of plant community structure in native rough fescue prairie. Then I describe in detail the soil insect fauna of that system, in search of patterns from which their impact on the plant community might be deduced.

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CHAPTER 2

EFFECTS OF INSECTS ON PRIMARY PRODUCTION IN TEMPERATE HERBACEOUS COMMUNITIES: A META-ANALYSIS

Introduction

Though insects are ubiquitous in herbaceous communities, their effect on primary production is much debated (Crawley, 1989; Carson and Root, 2000). By mass, insects outweigh vertebrates as much as tenfold in temperate terrestrial ecosystems (Pimentel and Andow, 1984), but may have little effect on primary production if their populations are limited by natural enemies (Hairston et al., 1960; Schmitz et al., 2000) or food quality, rather than food quantity (Hartley and Jones, 1997). Though most investigators measuring the effects of insects on primary production assert that they are measuring the effects of insect herbivory (Fraser and Grime, 1997; Carson and Root, 2000), insects fill additional ecological roles relevant to production, including accelerating nutrient cycling (Seastedt and Crossley, 1984; Blumer and Diemer, 1996; Belovsky and Slade, 2000) mediating plant competition (Clay et al., 1993; Ramsell et al., 1993), and predation (Moran and Hurd, 1998). Thus, it is not self evident that their net effect on plant growth should be negative. While agronomists have often drawn attention to the fact that insect suppression increases yield in sown pasture (White and French, 1968; Henderson and Clements, 1977), results in self-sown communities are more varied, with insects in some cases decreasing primary

production (Fraser and Grime, 1997; Carson and Root, 2000) but in others having no effect (Gibson et al., 1990; Coupe and Cahill, unpublished).

This variability in response could depend upon several attributes of the community. These include bottom-up influences such as the food quality of its constituent plant species and top-down influences, such as the traits of the dominant insects, and abundance and effectiveness of natural enemies.

Productivity has been proposed as one factor modulating the relative strengths of bottom-up and top-down influences on herbivore numbers (Oksanen et al., 1981). For example, systems with low productivity contain lower food supply, and plants of lower food quality and palatability (bottom-up control; Coley et al., 1985; Ritchie, 2000), retarding growth of insect herbivore populations, and lessening their potential to directly influence primary production (Olf and Ritchie, 1998). Alternatively, insect herbivores in more productive plant communities may experience greater population control from natural enemies, which could reduce their impact on plant growth (Fraser and Grime, 1997). If both top-down and bottom-up factors operate simultaneously, then insects should impact primary production most at intermediate productivity. These hypotheses lead to 3 mutually exclusive predictions of the relationship between primary production with and without insect herbivory (Fig. 2.1a).

The effects of insects on primary production may also be influenced by plant species diversity. This topic has been of interest to agroecologists who seek to understand why pest outbreaks are more frequent in monocultures than in polycultures (Andow, 1991). Root (1973) hypothesized that in more diverse

agricultural communities, population density of specialist insect herbivores is limited by decreased foraging efficiency (the resource concentration hypothesis), or greater abundance and effectiveness of natural enemies (the natural enemies hypothesis). These hypotheses have been supported by studies showing lower specialist insect herbivore abundance and greater natural enemy abundance in polyculture (Altieri et al., 1985; Schellhorn and Sork, 1997). However, outbreaks are relatively rare in any particular site, and as they involve single species of insects, they are in contrast to the diverse suite of insects (and plants) that typify natural herbaceous communities (Faeth, 1987). The prediction that insects will have a lower proportionate effect on primary production of more speciose plant communities has yet to be tested across a wide diversity of insect herbivore pressure and plant community types.

Community type could also affect the response of plants to insect removal. Strong et al. (1984) described the conceptual gradient between communities as random assortments of populations with little density dependence and fluctuating species composition, and predictable systems maintained by tight interspecific competition, with little top-down control of insect herbivores. They maintain that insect community composition correlates with plant community composition in some cases (*Spartina* saltmarshes) though not in others (bracken fern patches). Root and Cappuccino (1992) found large temporal variability and little intraguild competition in the insect communities of botanically similar old fields. However, even if insect communities show limited concordance with plant communities, I suggest that the effects of insects on primary production could depend upon

community type, if dominant plant species vary in palatability, susceptibility to herbivore attack, herbivore type, or natural enemy numbers.

A common technique used by investigators to address community-level impact of insect herbivory is chemical exclusion with insecticides (Clements et al., 1987; Brown and Gange, 1992). Community response measures such as plant cover and biomass are compared between sprayed and unsprayed plots. This method examines effects of all insects, without excluding elements of community regulation such as disturbance, grazing, and natural abiotic conditions. Despite a growing body of research using this approach, a quantitative synthesis of the effects of chemical exclusion of insects on the productivity of herbaceous communities is lacking. A meta-analysis was used to test the following questions:

- 1) What is the average effect size of insect suppression on total above-ground phytomass?
- 2) Does effect size vary as a function of plant species composition?
- 3) Is the effect size modulated by primary productivity?
- 4) Is there a correlation between effect size and plant species richness?
- 5) does the effect size depend upon outbreak status?

Methods

Literature search and paper selection

I conducted a search for experiments in which insecticides were used to examine the effect of insects on above-ground net primary production of a temperate herbaceous plant community. My search methods were chosen to

locate papers that had used this method, regardless of the goals of the study (e.g. applied vs. theoretical) or study system.

I used two primary sources. (1) The Web of Science (1975-2002). This is a citation database of scientific papers from multiple disciplines, including ecological and agronomic journals. A list of the keyword combinations (with justification) and author searches used is included in Appendix 1. (2) Biological Abstracts (on paper) from 1950-1983. I searched the section "Economic Entomology: Field, Flower, and Truck Crops". I then searched the electronic Biological Abstracts (1984-2001) using the same keywords as above (Appendix 1). The literature cited by these studies was also searched for additional potential papers for inclusion. As I repeatedly found the same publications with these different search methods, I conclude that this search has captured most of the peer-reviewed published papers on this topic in English. While it would have been desirable to include papers published in other languages, this would have necessitated a unique, comparable, set of keywords for each additional language, and would have entailed the risk of incorrect translation. I also include data from our own ongoing research program at Kinsella (Coupe and Cahill, unpublished), and unpublished data from two other studies (Bowers 1976, Gibson et al., 1990).

Each paper was reviewed to see if it met the following selection criteria:

- (1) The study included measures of community phytomass at the study plot level. If data were separated by constitutive parts (life-form, species, etc.), they were summed to obtain a plot level measure. Studies that examined the response only of a single species to insect suppression were rejected, since the goal was to

measure community-level processes. (2) The study was conducted outdoors, in a natural system. Agricultural crops, microcosms, mesocosms, and greenhouse studies were excluded. *A priori* exclusion of studies due to species composition was not made, so communities could consist of native or introduced species. I located 24 acceptable studies, providing 66 data points (Appendix 2). As there was a preponderance of studies in pasture, I caution that this dataset is a non-random selection of herbaceous communities and the conclusions may not be applicable to all temperate systems.

Data acquisition and Classification

Since some studies reported data from more than one site, I considered study sites independent data points if they showed strong differences in botanical composition, and/or they were separated by at least 5 km. Several studies had more than one treatment, but only the treatment using the broadest spectrum insecticide (most insects affected) was compared with the control (no insecticide). When more than one broad spectrum insecticide was used, I chose the one with the least known impact on non-target organisms (such as nematodes, earthworms, and molluscs). Non-target effect information was obtained from within that paper and others in the meta-analysis whose authors used the same insecticide. I present results from the peak control phytomass (grams dry weight/m²), measured during the first year for which data were available. Phytomass was reported as annual yield in some cases (sown pasture) and as standing crop in others (some pasture, grassland, all forb-dominated communities). Annual yield is a compounded

measurement of production from several harvests of standing crop in the same location, so measurements of yield and standing crop could not be combined for all analyses. As the interval between the initiation of spraying and biomass measurement varied between 21 days and 2190 days in the studies, there is concern that effect sizes will be biased as a function of the duration of the study. However, for the full set of data there was no relationship between effect size and study duration ($F_{1,65}=2.929$; $r^2=0.043$; $P=0.092$), and thus no time-weighting was conducted, as has been necessary in other studies (Downing et al., 1999). It is important to note that it is unclear whether the lack of a relationship between time and effect size is itself interesting information suggesting that overall, insect effects on production do not get compounded through time, or a sampling artifact due the fact that 50 of the 66 measurements used were taken within the first season of insecticide application.

Each study site was assigned to one of 5 community types: young pasture, mature pasture, native grassland, mature forb, and young forb. Young pastures ($n=27$), were defined as graminoid-dominated communities sown with grazing-adapted grasses such as *Lolium*, and with clover, less than 10 years old. As a consequence of their recent establishment from sown seed, species diversity tends to be low. Mature pastures ($n=27$) were defined as graminoid-dominated communities also sown with grazing adapted grasses, but allowed to grow for at least 10 years prior to the study, during which forbs and grasses not part of the original seed mix were able to establish. Native grassland ($n=3$) was defined as a perennial-dominated, community, composed primarily of graminoids and not

sown from seed. Examples included untilled prairie (e.g. Chapter 3; Gibson et al. 1990) or chalk grassland (Fraser and Grime, 1997). Mature forb communities (n=6) were defined as plant communities not in early succession whose biomass was dominated by forbs, typically perennials. In our dataset these were either an old field in the eastern United States (Carson and Root, 2000) or one of 5 communities in an upland dale (Fraser and Grime, 1997). Age was not used as a criterion to classify mature forb communities because that information was generally not provided, unlike in pasture systems. Young forb communities (n=3) were defined as self-sown communities, dominated by forbs, early in succession, established by removing mature plant communities; annuals form a large proportion of the phytomass (e.g. Brown et al., 1987). Sites were also classified according to whether or not an outbreak occurred there during the study. Outbreaks, which are population irruptions of a single species of insect herbivore, were described as such by the investigators, rather than interpreted from the results; the term "infestation" was also interpreted to indicate an outbreak. Outbreaks were reported in 5 of the 66 sites.

Species richness measures were derived from tables and graphs, and were available for 32 sites. Most anecdotal accounts of plant species richness were not used, unless they supplemented data from tables or graphs, or resulted from personal communication with the author (Wilson et al., 1995). When biomass or cover measures were given, they sometimes included categories such as "grass weeds" or "dicots" recorded as minor components of the community (Henderson and Clements, 1977). Unless there was more detailed information in the text,

each was conservatively scored as one species. Thus in all cases I have used a minimum estimate of species richness.

Statistical analyses

In order to contrast methods for making generalizations about the effects of insects on primary production, I began with a vote count. Studies were scored according to whether or not individual experiments rejected the null hypothesis at $P < 0.05$. I then proceeded with more sophisticated meta-analytical methods. Our metric of effect size is the log response ratio (L), the natural log of the ratio (R) between the mean phytomass of the sprayed (X_S) and control (X_C) groups ($\ln(R) = \ln(X_S/X_C)$; Hedges et al., 1999). Thus, L expresses the proportional effect of insect suppression on phytomass, with positive values indicating greater phytomass in sprayed plots. The best approach to meta-analysis of numeric data incorporates measures of both mean, and variability around the mean, of each data point (Gurevitch and Hedges, 1999). However, the majority of studies did not provide measures of variability. Therefore, I conducted two separate analyses: one using just the studies providing measures of variability and sample size ($n=15$), and one with all 66 data points, treating individual experiments as single data points throughout (Gurevitch and Hedges, 1999).

MetaWin 2.0 (Rosenberg et al., 2000), was used for analyses of the data for which measures of variability were available. I used a structured random-effects model which assumes a random component of between-study variation in means in addition to variation in means due to sampling error (Rosenberg et al.,

2000). Habitat type (e.g. mature field, young forb) served as a categorical variable in the model. For the confidence interval, I calculated a bootstrapped effect size estimate (Adams et al., 1997), presented in the text as a back-transformed (unlogged) value. I set our α value at 0.01 to account for the inefficiency of log response ratio equations in avoiding Type I errors at sample sizes lower than 20 (true probability content as low as 91% with $\alpha=0.05$; Hedges et al., 1999). Although I present this result as a 95% confidence interval, the true probability content is unknown, and likely slightly different. For the full data set (including those measures that lacked estimates of variability) I performed an ANOVA using SPSS 10.0 (SPSS Inc., 2000). Community type and outbreak status were treated as fixed factors with L as the response variable. A planned post-hoc comparison of means was made between young pasture and mature pasture, the two habitat types for which the most data were available.

The most direct way to determine whether the net effects of insects on plant growth varied as a function of productivity would be to perform a simple regression between effect size (L) and productivity. Unfortunately, as L is calculated as the ratio between unsprayed and sprayed plot biomass, and the sprayed plot biomass is the surrogate measure of productivity in these herbaceous communities (Knapp et al., 1998), this would result in a regression which includes the same data in both axes, and could force a significant negative relationship between L and sprayed biomass even with simulated data (Jackson, 1997). As a result, an alternative method of analysis was needed in which I could avoid the use of ratios and directly determine the form of the relationship between sprayed

and unsprayed biomass in each site. If insects have no net effect on plant growth at any level of productivity, then there should be a linear relationship with a slope=1 between sprayed and unsprayed biomass. If insects have a constant proportional effect on primary production, independent of productivity, the relationship will be linear with a slope less than 1. Increasingly negative effects with productivity are indicated by a significant and negative quadratic term, while decreasingly negative effects would be indicated by a significant and positive quadratic term. A unimodal relationship between productivity and the proportional effects of insects on plant growth would result in a sigmoid relationship between sprayed and unsprayed biomass, and would be indicated by a significant cubic term in the regression (Fig 2.1a).

Describing the relationship between two variables is notoriously difficult and thus I chose to use two methods: (1) a stepwise regression, and (2) a generalized additive model (GAM). In both analyses, above ground biomass in the control plots treated served as the response variable, and biomass in the sprayed plots served as the independent variable. In the stepwise regression, I also included the squared and cubed terms of sprayed biomass as independent variables, added in that order (linear, quadratic, cubic). Following the methods of Cahill and Casper (2000), I tested whether adding the quadratic or cubic terms significantly increased the F ratio of the model. The GAM was run using a spline with 3 DF, testing whether the inclusion of this non-linear term significantly improved the fit of the model compared to a simple linear relationship. The GAM allows a more powerful method of detecting non-linearity than the stepwise

regression, which is important here as I will infer biological meaning from the observed relationship. The stepwise regression was run in SPSS 10.0 (SPSS Inc 2000), and the GAM was run using PROC GAM in SAS 8.2 (SAS Institute 2002). Both analyses were run separately for standing crop and annual yield.

I tested the effects of plant species richness on L also using stepwise regression and a GAM. In these analyses, the ln-transformed species richness (and a quadratic term) served as the independent variable(s), and L served as the response variable.

One critique of using chemical suppression in ecological experiments is that effects on non-target organisms can lead to incorrect interpretations (Wall and Reichman, 2000). Organisms other than insects were affected by some insecticides in this analysis (Clements et al., 1982; Shure, 1971). I recorded all papers whose authors reported effects on earthworms or nematodes, or used an insecticide for which such non-target effects were found in another study, as this was the most common non-target effect. Studies using such insecticides found lower effect sizes ($t=3.69$; $df=36$; $P=0.001$) than studies using other insecticides, and thus our estimates of insect effects are likely underestimates of the "true" effect.

Results

Average effect sizes in different habitats

Twenty of the 66 sites reported a significant negative effect of insects on plant biomass, with only a single study reporting a significant result in the

opposite direction (Clements et al., 1982). Analysis of the effect sizes indicated that on average, insect suppression significantly increased above ground primary production (Fig. 2.2; Full data set (unweighted): $R = 1.151 \pm 0.057$ (95% CI); Partial data set (weighted by variance): $R = 1.23 \pm 0.18$ (95% CI).

Effect size varied between community types (Fig. 2.2; $F_{4,61}=3.230$, $P=0.018$), but there was significant non-homogeneity of variances ($F_{4,62}=4.813$; $P=0.002$). This variability appears driven by the mature forb communities as when they were removed, the remaining variances were homogeneous ($F_{3,56}=1.051$; $P=0.337$) and there was no community effect ($F_{3,56}=2.162$; $P=0.103$). Random removal of 6 studies from the dataset indicates that this change was not due simply to a loss of statistical power, suggesting the effects of insects on production in mature forb communities are different from their effects in the other community types. Effect sizes did not differ between mature pasture and young pasture (Tamhane's T_2 ; difference in averages $L=0.094$; $P=0.226$). In the dataset with variation, habitat had no effect on effect size (Between-group heterogeneity (Q)= 1.22; $P_{\text{chi square}}=0.718$). Insect suppression during insect outbreaks resulted in a greater proportional increase in production than did suppression in non-outbreak communities ($F_{1,64}=32.173$; $P<0.0001$). I note that of the 5 outbreaks which occurred, 4 occurred in young pasture.

Productivity and species richness

In the analyses to determine whether the effects of insect suppression vary with productivity, a linear relationship best describes the relationship between

sprayed and unsprayed biomass and yield in both the stepwise regression (Table 2.1; Figs. 2.1b, c), and generalized additive model (Table 2.1), indicating insects have a constant proportional effect on plant growth, independent of productivity.

Similarly, a linear term best explains the relationship between effect size and species diversity in both the stepwise regression (Table 2.1; Fig. 2.3) and GAM (Table 2.1). This indicates the proportional effect of insects on productivity are independent of plant species richness.

Discussion

Average effect sizes and habitat type

On average, insects reduced shoot biomass 15-20% in these temperate herbaceous communities. That biomass tends to be higher in treated plots suggests that herbivory is the dominant direct mechanism by which insects affect primary production in these systems, and I will frame the discussion in that context. These values should be taken as a minimum effect of insect herbivory in these systems, as (1) chemical suppression does not result in complete insect exclusion, and (2) insects also perform functions that can increase plant growth (e.g. predaceous insects; Moran and Hurd, 1998), reducing the magnitude of the overall net effect. This magnitude of tissue loss due to insects is similar to that found in temperate forests (5-15% leaf area removed; Landsberg and Ohmart, 1989), but far less than the 35% yield loss reported globally in agricultural systems (Pimentel and Andow, 1984). However, the hypothesis that insects decrease primary production to some degree has been in less doubt than the

various hypotheses proposing that these effects vary as a function of community traits.

Overall, community type had no effect on mean effect size. This conclusion agrees with Landsberg and Ohmart's (1989) study showing uniformity in insect defoliation across many forest community types. However, the significantly greater variance in mature forb communities suggests that community type does modulate insect impact on primary production, but not in a fashion predictable from the existing data. As a group, graminoids have lower investment in chemical defences than dicotyledons, higher investment in structural defences, lower nitrogen concentrations, and greater tolerance to herbivory (Tschamtkke and Grieler, 1995). Bigger and Marvier (1998) showed that invertebrates have a strong negative effect on forb growth, especially in comparison with vertebrates, while Moran and Hurd (1998) found that biomass of grasses, but not of forbs, was increased by addition of a top arthropod predator to an old field. Although the larger average effect size in young pasture than in mature pasture was not significant, the relative frequency of outbreaks in young pasture suggests that these two community types are affected differently by insects. It is noteworthy that with its greater dominance of grazing-adapted plants, higher productivity, and lower species diversity (Clements et al., 1987), young pasture can be thought of as the most "agricultural" of all habitat types considered here. This is evidence for the hypothesis that some community types are more likely to be affected by outbreaks than others, but it should be noted that the explanations for outbreaks are not always directly related to plant community

properties; they include climate, changes in host plant quality, and insect population fluctuations (Berryman, 1987).

Effects of productivity

As the relationship between sprayed plot biomass and unsprayed plot biomass had no significant non-linear component, I conclude that the negative effect of insects on production does not vary as a function of productivity in these systems. This finding is not supportive of the hypotheses stating that top-down or bottom-up control of insect herbivores are dependent upon productivity. The original advocates of the idea that top-down control varies as a function of productivity (Oksanen et al., 1981), proposed that this phenomenon was most likely for relationships between plants and endotherms, arguing that invertebrates were more likely to be regulated by temperature than productivity per se. In a later review of the model and its evidence Oksanen and Oksanen (2000) stated that not enough is known about the effects of folivorous insects on primary production to judge whether the model is applicable to them. Indeed, individual studies do suggest that the effects of top-down and bottom-up forces on insect herbivores and primary production do vary as a function of productivity. Fraser and Grime (1997), examined the Oksanen and Fretwell model (top-down control) for insects and found that insect impact on primary production was greatest at intermediate levels of productivity, while Ritchie (2000), showed that insect herbivore populations were limited by food quality in N poor environments, but not limited by top-down forces in more productive environments. However, this

meta-analysis reveals that overall, the effects of insects on plant growth are independent of productivity. A similar conclusion was made by a recent meta-analysis of invertebrate effects on cover and biomass (Schädler et al., 2003), although their analysis included biomass in effect size calculations and on the x axis, the potential confound discussed in our methods section (Jackson, 1997). I caution that any conclusion on this topic is clouded by our lack of knowledge of insect herbivore effects on root productivity, which in grasslands, constitute an average of 53% of annual productivity (Gill and Jackson, 2000). Although above ground insect herbivory is known to reduce root growth (Cain et al., 1991, Burselen and Hewitt, 1982) no studies have evaluated differences between habitats or along a productivity gradient, in the effects of insect herbivory on roots.

Effects of species richness

The lack of a relationship between species richness and response to insect suppression suggests that even if plant diversity affects specialist herbivore load or natural enemy attack rate, these differences do not translate to effects on primary production. Comparison of this result with the effects observed in agricultural systems is difficult because yield response to diversity manipulation is rarely measured (Risch, 1987), and when it is, non-crop plants are not considered as contributors to yield (Altieri et al., 1985; Schellhorn and Sork, 1997). In natural systems, Root's (1973) resource concentration hypothesis has been supported by studies finding greater defoliation (Kamata, 2000) and

mortality (Cappuccino et al., 1998) of the tree hosts of monophagous insects, when those hosts were growing in habitats with lower tree diversity or isolation. However, when Mulder et al. (1999) manipulated plant diversity in a grassland, they found that insect impact on production was actually greater at higher diversity. A companion study found no support for the prediction that natural enemies would become more abundant at higher diversity (Koricheva et al., 2000). Significantly, the species composition of the plant mixtures was far more important to invertebrate abundance and trophic level composition, with the presence of nitrogen-rich legumes having the strongest effect.

Summary of results

Insects consistently depress primary production in a variety of temperate herbaceous communities. More studies are necessary to determine how community types differ (particularly in mature forb communities, where effects are most variable), but there is evidence that herbaceous community type is important to the magnitude of insect impact. The mechanisms for these community type effects are unclear, and they may include differences in the plant community (palatability, susceptibility to herbivory) or the insect community (feeding mode, rates of population growth), or both. I have presented evidence that these patterns are not affected by productivity or species diversity, two fundamental traits often used to describe plant communities.

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Table 2.1. Results from stepwise regression (SWR) and generalized additive models (GAM) describing the relationship between the effects of insect suppression on production and (1) productivity, and (2) plant species richness. Both SWR and GAM were used to determine whether the relationships between the effect and response variables are linear or non-linear. All linear models for the productivity regressions were significant ($p < 0.0001$), and the goal of that analysis was to determine whether the addition of the higher order terms significantly improved the fit of the model. The significance of the change in model fit was determined using the change in the F statistic in the SWR, and by using a chi-square, and thus "change" below refers to actual value of the change in F due to the addition of higher order terms in the SWR, or the chi-square value comparing the GAM with a 3 DF spline to the GAM without the spline. P_{change} refers specifically to the significance of the change in model fit due to the addition of the higher order term.

		Productivity				Plant Species Richness			
Biomass	SWR	Term	Parameter	F _{DF}	Change	P _{change}	Parameter	F _{DF}	P _{change}
			Estimate				Estimate		
		Linear	---	412.5 _{1, 22}	---	---	---	---	---
		Quadratic	---	413.1 _{1, 21}	0.527	0.476	---	---	---

		Cubic	---	414.3 _{1,20}	1.232	0.280	---	---	---	---
	GAM	Linear	0.757	---	2.96	0.398	---	---	---	---
Yield	SWR	Linear	---	7099.7 _{1,38}	---	---	---	---	---	---
		Quadratic	---	7101.8 _{1,37}	2.130	0.153	---	---	---	---
		Cubic	---	7101.9 _{1,36}	0.017	0.897	---	---	---	---
	GAM	Linear	0.8815	---	3.42	0.331	---	---	---	---
All data	SWR	Linear	---	---	---	---	---	---	---	---
		Quadratic	---	---	---	---	---	1.237	---	0.275
	GAM	Linear	---	---	---	---	0.0317	---	3.079	0.380

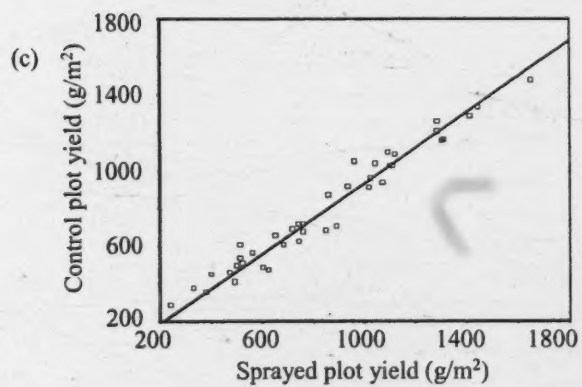
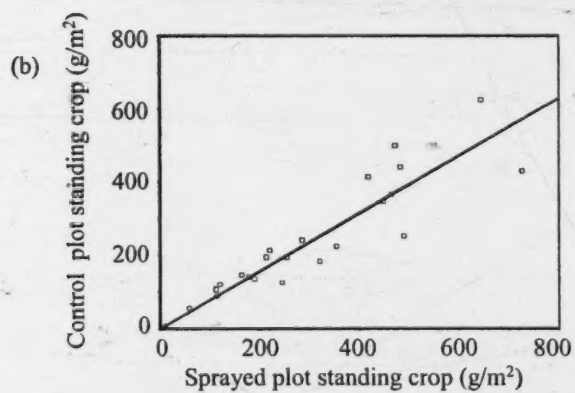
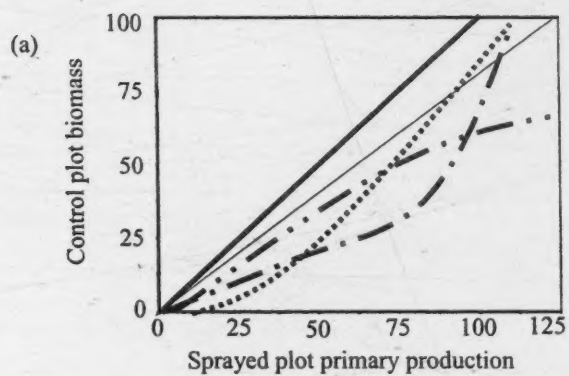


Figure 2.1. Models and data depicting the relationship between primary production with and without insecticide application. (a) Alternative models of how the relative strength of herbivory should vary with productivity result in distinct predictions on the form of the relationship between plant biomass in sprayed plots and unsprayed plots. (1) If insect suppression has no effect on plant growth there should be a linear relationship between control plot biomass and sprayed plot biomass with a slope = 1 (————). (2) If there is a constant proportional increase in primary production due to insect suppression, then there will be a linear relationship between sprayed plot biomass and control plot biomass, with a slope < 1 (————; 25% shown here). A quadratic relationship indicates either (3) an increasing effect of insect suppression at higher productivity (— · · —; bottom-up control), or (4) a decreasing effect of insect suppression at higher productivity (······; top-down control). (5) If both top-down and bottom-up processes strongly influence herbivory, there should be a cubic relationship between sprayed and unsprayed biomass (— · —). (b) The observed relationship between primary production of sprayed and unsprayed plots for standing crop data. (c) The observed relationship for yield data. In both b and in c, neither the quadratic nor the cubic terms significantly improved the fit of the model.

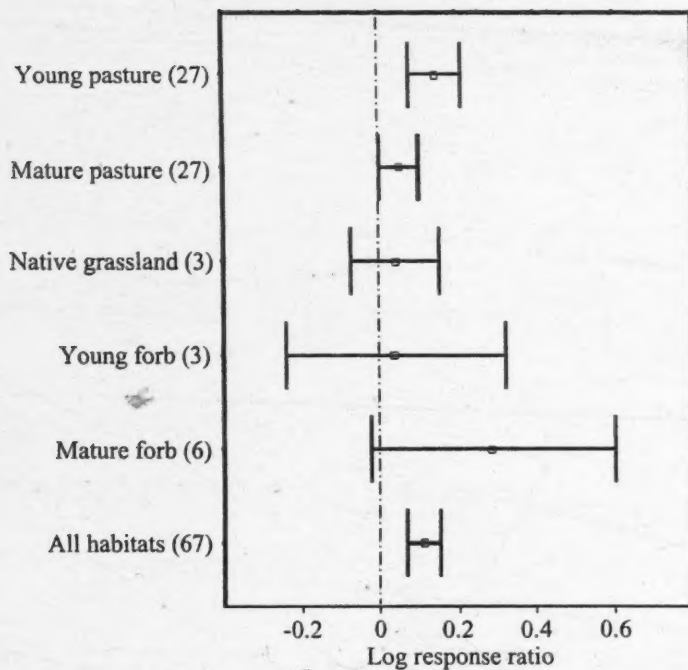


Figure 2.2. Estimated effect sizes due to insect suppression for each community type in the full (unweighted) data set (95% CI). The dashed line corresponds to no effect. Mean effect sizes do not vary between community types.

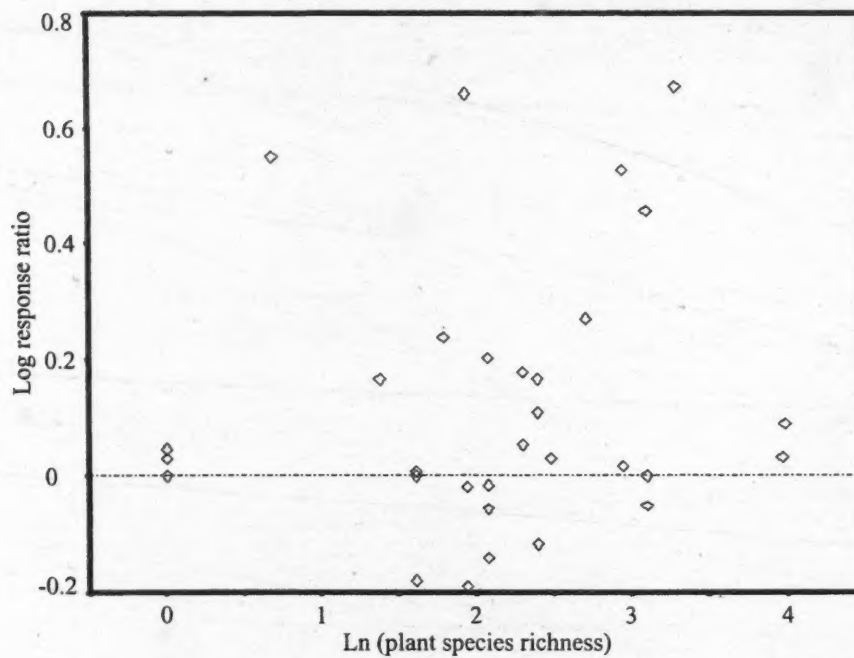


Figure 2.3. The relationship between plant species richness and the effect size associated with insect suppression. Neither the linear nor quadratic terms were significant in the stepwise regression or generalized additive model (Table 2.1), indicating the net effects of insects on above-ground primary production are independent of plant species diversity.

Appendix 1. Literature search criteria.

Web of Science searches:

I used the following key word combinations: "insect herbivory and biomass", "insect herbivory and diversity", "insecticide and biomass", "insecticide and herbivory", "herbivory and diversity", "insect herbivory and succession", "insecticide and succession", "insect herbivory and insecticide", "insect herbivory and grassland", "insect herbivory and root", "pesticide and grassland", and "insect and grassland".

I chose these keywords mindful of the diverse goals that ecologists and rangeland researchers are likely to have had in conducting these types of experiments. Thus ecologists have used this method to investigate insect herbivory, diversity, root performance, and succession, while rangeland researchers have used this method to examine effectiveness of insecticides or pesticides, predominantly in pasture.

I also searched authors for: Brown V.K., Cain M.L., Cantlon J.E., Carson W.P., Clements R.O., Gange A.C., Lawton J.H., Louda S., Maron J.L., Masters G.J., Olff H., Ritchie M.E., Root R.B., Seastedt T.R., Siemann E., and Tilman D.

All of the above authors had either conducted studies using this method that were already included in the analysis, and located using other methods, or they had a history of research in the field of plant-insect interactions.

Appendix 2. List and description of all experiments used in this study.

Source	Habitat	n	outbreak status	plant species richness	control plot phytomass (g/m ²) +/- SE ^a	sprayed plot phytomass (g/m ²) +/- SE ^a
Standing crop measured						
Blackshaw 1984; table 2: site 1	mature pasture	6	No		195.8 +/- 12.8	255.5 +/- 12.8
Bowers 1976; fig. 10	mature pasture	5	No		346.7	448.6
Brown et al., 1987; table 1	young forb	10	no	5	414.2 +/- 77.5	417.7 +/- 79.3

Carson & Root 1999, fig 3	young forb	30	no	22	499 +/- 26.8	473 +/- 26.0
Carson & Root 2000; fig. 7	forb dominated	15	yes	19	429 +/- 12.8	727 +/- 40.0
Coupe & Cahill 2001; unpublished data	native grassland	10	no	53	214 +/- 12.9	221 +/- 13.6
Dondale 1972; table 3: field 1	young pasture	7	no		5940 ^d	6820
Dondale 1972; table 3; field 2	young pasture	7	no		5980	6400
Dondale 1972; table 3: field 3	young pasture	7	no		3800	5300
Ellis et al., 1990; table 6: North Wyke	mature pasture	5	no		147	163
Fraser & Grime 1997; fig. 1: site 1	mature forb	10	no	1	10 +/- 1.0	10 +/- 1.0

Fraser & Grime 1997; fig. 1: site 2 -	native grassland	10	No	5	57.5 +/- 0.8	57.5 +/- 1.3
Fraser & Grime 1997; fig. 1: site 3	mature forb	10	no	27	125 +/- 4.0	245 +/- 6.7
Fraser & Grime 1997; fig. 1: site 4	mature forb	10	no	22	225 +/- 4.7	355 +/- 2.9
Fraser & Grime 1997; fig. 1: site 5	mature forb	10	no	1	625 +/- 7.2	645 +/- 6.8
Fraser & Grime 1997; fig. 1: site 6	mature forb	10	no	1	107 +/- 2.6	112 +/- 2.4
Gibson et al., 1990; unpublished data	native grassland	8	no	54	441.0 +/- 17.5	482.6 +/- 27.3
Goldson and Trought 1977	young pasture	7	yes		136.6	189.5
Martin 1974; table 5	young pasture	4	no	22	120	120

Newbold 1981; table 1: Burrowland	young pasture	5	no	195	212.7
Newbold 1981; table 1: Grange of Cree	young pasture	5	no	90.2	113.4
Schmitz 2002; pers. comm.	mature forb	10	no	18	132.7 +/- 12.6
Shure 1971; fig. 4	young forb	2	no	11	286 +/- 33.2
Wallace and Mahon 1952; table 1	young pasture	5	yes	7	489.9
White and French 1968; table 6: Mitford	young pasture	6	yes	2	321
White and French 1968; table 3: Blagdon	young pasture	6	yes	6	465

Annual yield measured

Barker et al., 1984; table 2	4	no	4	628.2	742.3
young pasture					
Clements et al., 1982; table 2:	4	no		460	470
Pwllpeiran High					
mature pasture					
Clements et al., 1982; table 2:	4	no	7	290	240
mature pasture					
Liscombe High					
mature pasture					
Clements et al., 1982; table 2: Corwen	4	no	10	360	380
mature pasture					
Clements et al., 1982; table 2:	4	no	8	380	330
mature pasture					
Macclesfield					
mature pasture					
Clements et al., 1982; table 2:	4	no	10	410	490
mature pasture					
Ostrwaldtwistle					
mature pasture					
Clements et al., 1982; table 2: Redesdale	4	no	11	450	400
mature pasture					
Clements et al., 1982; table 2: Penrith	4	no	8	490	600
mature pasture					

Clements et al., 1982; table 2: Brecon	4	No	5	500	500
Clements et al., 1982; table 2: Pwllpeiran Low	4	No	8	540	510
Clements et al., 1982; table 2: Llysfasi	4	No	7	570	560
Clements et al., 1982; table 2: Liscombe Low	4	No	5	610	510
Clements et al., 1982; table 2: Clunton	4	No	11	610	680
Clements et al., 1982; table 2: Selside	4	No	8	660	650
Clements et al., 1987; table 2: Level Crossing	5	No	19	513	521
Clements et al., 1987; table 2: Canal	5	No	12	694	716
Clements et al., 1990; table 2: Exminster	4	No		680	760

Clements et al., 1990; table 2: Highclere	mature pasture	4	No	710	890
Clements et al., 1990; table 2: Great Alne	mature pasture	4	No	720	760
Clements et al., 1990; table 2: Pant-y-dwr	mature pasture	4	No	940	1070
Clements et al., 1990; table 2:	mature pasture	4	No	1030	1100
Barnard Castle					
Clements et al., 1990; table 2: Winterburn	mature pasture	4	No	1030	1110
Clements et al., 1990; table 2: Ponterwyd	mature pasture	4	No	1100	1090
Ellis et al., 1990; table 6: Tadcaster	mature pasture	5	No	142	178
Henderson & Clements 1974; table 2	mature pasture	4	No	719	740
Henderson & Clements 1977; table 1:	young pasture	6	No	685.5	849.7

Devon									
Henderson & Clements 1977: table 1:	young pasture	6	No	875.5	858.7				
Essex									
Henderson & Clements 1977: table 1:	young pasture	6	No	915	1016				
Lancashire									
Henderson & Clements 1977: table 2:	young pasture	6	No	918.9	934				
Leicestershire									
Henderson & Clements 1977: table 2:	young pasture	4	No	962.3	1020.5				
Kent									
Henderson & Clements 1977: table 2:	young pasture	6	No	1041.4	1042.9				
Yorkshire									
Henderson & Clements 1977: table 2:	young pasture	6	No	1089.8	1118.8				
Northamptonshire									
Henderson & Clements 1977: table 2:	young pasture	4	No	1163.4	1301.6				
Wiltshire									
Henderson & Clements 1977: table 2:	young pasture	6	No	1165.2	1309.5				

^bThe insecticides used above with this non-target effect are aldicarb, methiocarb, and Temik.

^c Standing crop values from Dondale 1972 were not used in productivity-effect size analysis due to low drying temperature of vegetation samples

CHAPTER 3

THE EFFECTS OF INSECT HERBIVORY ON PLANT COMMUNITY STRUCTURE AND PRIMARY PRODUCTION OF NATIVE GRASSLAND

Introduction

Insects are often dominant in biomass to vertebrates in terrestrial ecosystems (Watts et al., 1982; Pimentel and Andow, 1984), but are generally considered less important to ecosystem function and plant population dynamics (Strong et al., 1984; Crawley, 1989a). Insect population sizes are thought to be limited by their natural enemies (Strong et al., 1984; Schmitz et al., 2000), while the prevalence of plants with low food quality, and structural or chemical defences (Schoonhoven et al., 1998), limits the direct impact that insect herbivores can have on primary production (Hartley and Jones, 1997). One way to approach this debate is to begin with a distinction between effects during and shortly after insect herbivore outbreaks, and the effects of the more diverse suite of insect herbivores in non-outbreak conditions (Faeth, 1987). When outbreaking insect populations attack a dominant member of the plant community, they may decrease primary production (White and French, 1968; Maron and Jefferies, 1999; Carson and Root, 1999) alter the trajectory of succession (Carson and Root, 2000), facilitate invasion by non-native plants (Maron and Jefferies 1999) or alter community composition (Ueckert, 1979; Lura and Nyren, 1992; Carson and Root, 2000). Conversely, in non-outbreak conditions, the effects of insects on plant community structure are mixed. Insects may strongly affect the course of early secondary

succession (Brown and Gange, 1992), or their effects can be so slight as to be nearly undetectable (Hendrix et al., 1988; Gibson et al., 1990; Coupe and Cahill, in press). Despite their predominance in nature (Barbosa and Schultz, 1987), it is under non-outbreak conditions that the least information is available on community impacts.

If food quality is a major factor limiting insect herbivore impact on herbaceous communities (Hartley and Jones, 1997), then it is reasonable to expect that gross differences between plant communities in defence and palatability will modulate the effects of insect herbivory. For example, grasses have lower levels of chemical defences and lower nutritional value relative to forbs (Tschamtkke and Greiler, 1995), and support a different insect herbivore fauna as a consequence (Denno and McClure, 1995). Although mature grassland is the dominant natural community type of 24% of the earth's land area (Huston, 1994), the greatest body of the evidence for insect herbivore impact on mature plant community structure comes from forb-dominated communities (McBrien et al., 1983; Fraser and Grime, 1997; Maron and Jefferies, 1998; Carson and Root, 2000; Schädler et al., unpublished). If insect herbivore impact is dependent upon plant species composition, then findings from forb-dominated communities are unlikely to be representative of the effects of insects on graminoid communities.

Evidence for insect impact on grassland communities comes almost entirely from highly productive pasture dominated by *Lolium* spp. (Coupe and Cahill, in press). These studies have generally shown that insect suppression increases primary production, but they have not measured shifts in plant

community composition. As insects may affect community composition while having no effect on cover (Huffaker and Kennett, 1959) or primary production (Gibson et al., 1990) measurement of insect effects on species diversity, and performance of the dominant species, may more often reveal effects of insects on plant communities than could be observed solely by measuring their effects on plant biomass.

Productivity is another factor that may modulate the impact of insect herbivores on plant communities. For example, the impact of insect herbivores may be minimal in low productivity habitats (Fraser and Grime, 1997), due to the herbivore resistance exhibited by plants in low productivity communities, where plants are less able to recover following herbivore damage (Coley et al., 1985; Grubb, 1992). Under such conditions, insect herbivore impact may be limited to a few rare and palatable plants, and insect herbivory is expected to have a negative but negligible effect on plant species richness (Olf and Ritchie, 1998). In more productive habitats, plants may be better able to afford tissue loss through herbivory, and less able to afford constitutive plant defences if these compromise growth rate (Coley et al., 1985). However, the impact of insect herbivores on plant community structure is expected to be greater at lower levels of productivity if insect herbivore populations are better regulated by their natural enemies in more productive habitats.

In summary, there is a sparsity of information on community-level impacts of insect herbivory in graminoid-dominated communities of low productivity. Due to their different plant species composition from forb-

dominated communities, it may not be reasonable to infer effects of insect herbivores on community structure in such communities, in comparison with forb-dominated communities of similar productivity. Equally, it may not be reasonable to expect unproductive grassland to respond similarly to productive pasture communities. I conducted a two year experiment, examining effects of insect suppression on plant community structure in a native grassland of low productivity. In order to detect any subtle changes in community structure that may be caused by insect herbivory, I took several separate measures of plant community response in addition to the measures of primary production made by many previous researchers. The main objectives of this study were 1) to determine how above-ground primary production and root biomass are affected by insects, 2) to determine effects of insects on plant diversity, cover and species composition, 3) to examine effects of insects on growth and mortality of 6 of the most common plant species.

Methods

Study site

The study was conducted from May 2001- August 2002 at Kinsella Beef Cattle Research Ranch, a 3200 ha ranch north of Kinsella, in Beaver County, Alberta. The ranch is located in the aspen parkland ecoregion, which is typified by an undulating morainal landscape. The site itself (53.092° N, 111.552° W) is a self-sown grassland that has never been ploughed or tilled. It consists of two adjacent fields with a total area of 20 ha, and a gentle, south-facing slope,

bounded and separated by barb-wire fencing to exclude cattle. Both fields contain, and are bordered to the north, by clonal stands of aspen (*Populus tremuloides*), and have patches of the shrub *Eleagnus commutata* (wolf willow), interspersed with forbs and grasses. The majority of above-ground phytomass in this prairie plant community is graminoid (72%; Coupe, unpublished), but the majority of plant species (39 of 53 recorded; Coupe, unpublished) are forbs. Most (87%; Coupe, unpublished) of the phytomass is belowground. The soil is Elnora, a thin, well drained black chernozem typical of grasslands in the Viking Upland of Beaver County (Howitt, 1988). At the outset of the study, the site had been grazed each fall by cattle for 20 years, but cattle were excluded for the duration of the study. White-tailed deer were seen regularly at the site.

The climate in this region is continental; 5 months of the year (Nov-Mar) have average daily temperatures below 0°C (Environment Canada), and most plant growth occurs between early May and late August (B. Irving, pers. comm.). 2001 and 2002 were unusually dry years. Precipitation during the growing season of 2001 and the prior winter was 186.6 mm, 56% below the 37 year average of 428 mm. Precipitation during the growing season of 2002 and the prior winter was 183.3 mm, 57% below the 37 year average of 428 mm (Fig. 3.1). Annual precipitation in these successive years was the lowest of the previous ten years for which data were available.

Experimental design

I used a complete randomized block design with 4 treatments: control (no insecticide), above-ground insecticide, below-ground insecticide, and both (above- and below-ground insecticides; Fig. 3.2). Each treatment was replicated once in 10, 16 x 20 m blocks. Within each block, each treatment was assigned randomly to one of 4, 6 x 8 m plots. A 1 m wide mowed buffer bordered each plot on all sides, such that each plot was separated by 2 m. In order to reduce reinvasion of insects into the sampling area, all vegetation sampling was conducted in the inner 4 x 6 m of each plot. All blocks were established more than 10m from a road, trail, or fence. No two blocks were separated by less than 25 m or more than 200 m. The areas of rough fescue prairie chosen were free of aspen (*Populus tremuloides*) or wolf willow (*Eleagnus commutata*).

Chemical exclusion of insects

Chlorpyrifos is the active ingredient of both insecticides employed in this experiment. It is a broad spectrum insecticide (Kenaga et al., 1965), whose mode of action is cholinesterase inhibition (Eto, 1974). Lorsban 4E (Dow Chemicals; 48% active ingredient) was sprayed in a water emulsion at a concentration of 2.8 mL/L for the above- ground treatment. In each application, all plots treated with above-ground insecticide received 4.2 mL of Lorsban 4E in 1.44 L of water. This concentration is recommended for control of adult grasshoppers in cereal crops (Johnson, 1998). It was very effective in suppressing the numerically dominant above-ground insect orders, as measured in 7 m sweep net transects made

diagonally across the study plots on several dates (Figs. 3.3a, b). It was also very effective in reducing chewing damage (see below). Control plots, and plots treated with the below-ground insecticide alone, received the same volume of water. In order to optimize the insecticide's efficiency and avoid contamination of unsprayed plots, spraying was conducted between 1100 and 1600 hours in dry conditions. Spraying was not conducted unless the wind was 15km/h or less. Plots were sprayed every 2 weeks, from May 10th 2001 until August 24th 2001; then from May 3rd 2002 until August 22nd 2002.

The below-ground insecticide was Lorsban 15G (Dow Chemicals; 15% active ingredient) a granular insecticide and acaricide. Each treated plot received 64 g of Lorsban 15G in 670g of sand carrier, at the rate recommended for control of white grubs in turfgrass (Johnson, 1998). It was released from a 1L plastic jar attached to a plastic broomstick. The below-ground insecticide was applied by sweeping this device in a 2 m wide, lateral arc, making 4 passes per plot. It was applied on May 10th 2001; July 11th 2001; May 3rd 2002, July 8th 2002, and August 22nd 2002. However, soil macroarthropods were not significantly affected by the granular treatment, and soil mites were only suppressed by the below-ground insecticide in May 2002. Thus, the mechanism for any effects of the below-ground insecticide treatment are unclear. The ecological importance of below-ground insects in this system, and the effects of the insecticides on them, is discussed elsewhere (Chapter 4).

A common critique of studies using chemical exclusion techniques is that the chemicals used may have phytotoxic or fertilization effects on the plants

themselves (Shure, 1971; Brown et al., 1987). Realizing this potential confound, I conducted growth chamber experiments on two plants native to the grasslands of this region: *Festuca hallii* Piper (plains rough fescue), and *Achillea millefolium* L. (yarrow). Above-ground and root biomass were not affected by any treatment (Appendix 1). Schädler et al. (unpublished) also found no direct effects of granular chlorpyrifos on biomass of two forbs. Furthermore, a fertilization effect is unlikely; the maximum cumulative amounts of phosphorus and nitrogen added to this system (chlorpyrifos molecular formula: $C_9H_{11}Cl_3NO_3PS$) throughout the experiment were 0.170 g/m^2 and 0.077 g/m^2 respectively. Phosphorus added at 8 g/m^2 did not affect plant growth in this community in the summer of 2000 (Cahill, pers. comm.). Rather than being released in an ionic form, the nitrogen contained in chlorpyrifos tends to remain in a stable, aromatic ring molecule ($C_5H_2Cl_3NO$) following hydrolysis in soil (Racke et al., 1996).

Community response measurements

Plant cover and biomass were used to describe plant community response. Percent leaf cover was measured by ocular cover estimation in 3 permanent sampling quadrats per plot, using the Braun-Blanquet scheme (Kent and Coker, 1992) in 2001 and exact estimates (to the percentage point) in 2002. Vegetation of different species overlapped, so cover could be greater than 100%. The 20 x 50 cm sampling quadrats ran east-west, parallel to the plot boundaries. These dimensions were chosen to balance the conflicting problems of edge effect in such subjective measurements, with the greater between-sample heterogeneity

associated with sampling plots having lower perimeter length for the same area (Krebs, 1999). Quadrat locations were marked with paired anchor pins. Prior to sampling, a portable wooden frame was placed between these anchor pins, to be used as a visual guide. Vegetation not rooted in the quadrat and pushed into it by the frames' placement was gently brushed outside the sampling area. Cover was measured on three occasions in 2001: May 17th, July 3rd, and August 19th, then on three occasions in 2002: May 10th, July 11th, and August 13th. Vascular plants were identified to species when possible; otherwise most identification was to the genus level. Grasses were not identified to species in May cover estimations, due to their low stature and lack of reproductive structures. During the drought of 2002, grasses not flowering were identified by their leaf structure; identification was likely less accurate as a result. Moss species, which were scarce and nowhere dominant or forming sporophytes, were recorded as "moss".

Light penetration, another measure of vegetative structure, was measured in the permanent sampling quadrats on August 18th 2002. I used an Accupar linear PAR / LAI ceptometer (Model PAR 80; Decagon Devices Inc.) in bright, sunny conditions within two hours of solar noon. Light intensity ($\mu\text{mol/s/m}^2$) was measured beneath the above-ground vegetation of each cover plot and immediately above it. Light penetration was calculated as the ratio of light under the vegetation to ambient light. Results were pooled at the plot level.

Plant biomass was measured in 2 samples per plot by cutting vegetation to the soil surface in a 10 cm x 1 m quadrat, its long axis running east-west, parallel to the plot boundaries. These dimensions were chosen because it was not difficult

to avoid cutting outside the quadrat area. Therefore it was possible to realize the benefits of longer, thinner quadrats in reducing between- sample heterogeneity without the potential observer bias associated with them (Krebs, 1999). The vegetation was cut using hand-held garden shears (Corona BP 3180 USA). As the vegetation was harvested it was placed into brown paper bags and air-dried. All forbs and shrubs were separated to species. Grasses were treated as a group because of the difficulties associated with identification from vegetative characters. After sorting, all plant samples were dried at 70 °C and weighed. Biomass harvests were never collected closer than 30 cm to a permanent sampling quadrat. Three harvests were taken during 2001 (May 5th, July 3rd, and August 23rd) but just one during 2002, due to the negligible biomass production (July 13th) during the extended drought.

Root biomass was estimated from soil cores (16 cm diameter, 10 cm deep) taken from quadrats simultaneously sampled for above-ground biomass (with the exception of May 2002). Roots were extracted from the soil by hand, while separating soil insects from soil and roots. The roots were then washed to remove any remaining soil. During both May harvests (May 5th 2001 and May 15th 2002), two cores were harvested, in order to sample the soil insect fauna more intensively. On other dates (July 3rd, and August 23rd), one core was removed per plot, to reduce disturbance. When two cores were removed per plot the results were pooled for statistical analysis.

Total biomass, the sum of root and shoot biomass, was calculated when the two measures were taken concurrently. This was the case for all 2001

harvests, but not for the 2002 harvests because root biomass was measured only in May and shoot biomass was measured only in July.

Focal plant experiment

In order to evaluate the effects of insects on plant performance, a focal plant experiment was conducted in the summer of 2002. Due to the ineffectiveness of the below-ground insecticide (Chapter 4), this experiment used only control plots and plots where above-ground insecticide was applied alone. Due to difficulties with identification of grasses, the species chosen were ramets of the 6 most common forbs: *Comandra umbellata* A., *Rosa arkansana* Porter, *Solidago missouriensis* Nutt., *Achillea millefolium* L., *Cerastium arvense* L., and *Aster falcatus* Lindl. Morphometric measures of plant performance taken were number of leaves and height (*Comandra umbellata*, *Rosa arkansana*, *Cerastium arvense*, *Aster falcatus*) or length of the longest leaf for plants with a basal rosette and no central shoot (*Solidago missouriensis*, *Achillea millefolium*). These measures were assumed to correlate positively with biomass production for that year, and we expected similar correlations between these morphometric measures and seed production. However, massive plant mortality precluded powerful tests of these hypotheses during the year of study, so the true relevance of these measures to plant performance in this experiment remains unknown. At each observation, plants were assessed as either alive or dead, based upon stem and leaf colour. Plants that survived until August 12th (57 of 285) were harvested and dried at 70 °C for measurement of above-ground biomass.

We measured insect damage by visually estimating the percent of total leaf area removed by chewing insects. Chewing damage was considered a good estimate of total above-ground insect herbivore pressure; sucking and galling insects (homopterans) are also present in this system, but were rare during 2002, with lower sweep net counts than chewing insects (Figs. 3.3 a,b), and smaller individual size (pers. obs.). Since insect damage showed strong non-homogeneity of variances between plant species, this variable was transformed to frequency (damage/no damage) for statistical analyses.

As I wished to minimize overall disturbance to the study plots, and to minimize touching of the focal plants, since this can affect rates of herbivory at this site (Hik et al., 2003) they were visited on just 4 occasions (May 29th, June 26th, July 12th, and August 12th for biomass harvest), and touched on only 2 prior to harvest (May 29th and June 26th).

Statistical Analysis

The effects of insects on primary production, species richness, and light penetration were analyzed using mixed model analyses of variance, with each treatment as a fixed factor and block as a random factor (Littell et al., 1996). All cover and biomass measures were taken on more than one occasion, so for these I used repeated measures analyses with time as a third fixed factor, though date-specific analyses were also conducted and are shown in the figures. When more than one observation was taken per plot (cover, above-ground biomass, light) the results for that plot were pooled and the plot-level average was analyzed. Years

were analyzed separately to satisfy the assumption of repeated measures analysis of an equal time span between measurements, and because year differences in cover and biomass were far greater than differences between treatment means. As I expected forbs and grasses to respond differently (Tschardtke and Greiler, 1995), additional analyses of the treatment effects on species richness and cover were conducted for each group separately in addition to pooled analysis. To achieve normality all proportional variables were arcsine-square root transformed, and skewed data such as morphometric measurements were log-transformed (Sokal and Rohlf, 1991).

The PROC MIXED procedure in SAS 8.02 (SAS Institute, 2001) was used for the above analyses. All possible fixed and random effect interactions were included in the initial model. An advantage of PROC MIXED is that it allows removal from the model of random effects that have little explanatory value, thus increasing the degrees of freedom available to detect significant fixed effects (Littell et al., 1996). The fixed effect output provides conventional F and P values, but the random effect output provides covariance parameter estimates for each random effect, where low values indicate random effects with less explanatory power. The absolute value of the -2 Residual log likelihood statistic, which tests goodness of fit of the entire model, increases when nonzero covariance parameter estimates are removed from the model. This increase indicates a reduction in the goodness of fit. Random effects are removed from the model until there is a reduction in its goodness of fit that is statistically significant. Specifically, random effects were removed until the difference

between the resulting and initial -2 Residual log likelihood statistic was no greater than 2.6, the critical χ^2 value in a test with one degree of freedom and $P < 0.1$, or twice the chosen α value of 0.05 (Littell et al., 1996).

The effects of insects on focal plant mortality and frequency of insect damage were analyzed using generalized linear mixed models for binomially distributed data (using the %GLIMMIX macro; Littell et al., 1996), separately for each date and species. Plant status (dead or alive) was the dependent variable, the insecticide treatment and focal plant were the fixed factors, and block was the random factor. Since plants were replicated within plots, the random effects model included an interaction term with plant nested within treatment and block. Due to high ramet mortality of *Cerastium arvense*, *Comandra umbellata*, *Achillea millefolium*, and *Solidago missouriensis*, mortality analyses were only conducted on observations of these species on June 26th and July 12th. *Rosa arkansana* and *Aster falcatus* had higher rates of survival, so mortality analyses were also conducted for these species' performance on August 12th. Morphometric measurements of the focal plants, and plant damage, were analyzed with the same factors, in repeated measures mixed model analyses of variance (as used for cover and biomass), but including focal plant as the nested term in the random effects model.

A generalized linear mixed model for binomially distributed data was also used to test for species and insecticide effects on plant damage. Damage frequency (damage/no damage) was the dependent variable and species and insecticide treatment were the fixed factors, with block as the random factor.

Because some species by insecticide groupings had no insect damage, it was not possible to run a full model with all species and both insecticide treatments. Therefore, I tested for a species effect by removing sprayed plants from the dataset, and for an insecticide effect by removing the rarely damaged species *Achillea millefolium* and *Cerastium arvense* from the dataset. The latter analysis also included species as a fixed factor, but since the rarely damaged species were not included this result for the species effect is a conservative one.

The effects of insects on floristic composition as measured by cover, were analyzed using the blocked multiple response permutation procedure (MRPP). Similarly to the t-test and one-way ANOVA, the purpose of MRPP is to detect differences between *a priori* groups. MRPP has two advantages over these methods: it makes no assumptions regarding the underlying data structure, and it can be used for multivariate analyses (Zimmerman et al., 1985), which will often detect significant differences between groups that are not detected by aggregate responses such as species richness (McCune and Grace, 2002). MRPP calculates distance measures between objects (in this case, plots), where distance is calculated from values for each variable (in this case, species cover values). The distance between two objects is calculated thus:

$$\Delta_{K,L} = \left[\sum_{j=1}^r (X_{Kj} - X_{Lj})^2 \right]^{1/2}$$

where r is the number of species seen on that sampling date, and K and L are plots, each with a value for cover of species j (which can be zero). The symbol v is a constant, in this case 1, providing euclidean distance measures (Zimmerman

et al., 1985). Distance measures are calculated for all plot pairs. The average value of within-group distance measures in the i th treatment is calculated thus:

$$\xi_i = \binom{n_i}{2}^{-1} \sum_{K < L} \Delta_{K,L}$$

where n_i is the number of objects in that group, in this case 10 for each treatment.

The MRPP statistic for the entire dataset, δ , is a combination of within group distance measures such that:

$$\delta = \sum_{i=1}^g C_i \xi_i$$

where g is the number of groups, in this case 4 treatments, and C_i is a positive constant specific to each group, whose sum is equal to 1, and whose individual values are equal to n_i/N , such that δ is weighted by within-group sample size.

Clearly, low values of δ indicate low within-group distance measures, suggesting significant group effects. P values are calculated by comparing the observed δ values with δ values generated by 2000 randomizations, assigning each plot to a randomly selected treatment. Approximations of the P value are obtained by comparing the observed δ with the distribution of randomly generated δ values; P is equal to the proportion of randomized δ values less than the observed value.

The blocked MRPP used here (also known as the MRBP) is a variant of the MRPP used for randomized block designs. It takes into account between-block variation by restricting the randomization to the same number of cases of each treatment per block as in the experimental design (Mielke and Iyer, 1982).

Unfortunately, this method does not accommodate more than one experimental

factor. I followed the advice of McCune and Grace (2002), and ran a separate model for each insecticide treatment; thus two models were run for each measurement date. Separate blocked MRPP's were calculated on the cover data from July and August of both years, with the treatments (above- and below-ground) as the groups. MRBP analyses for May of 2001 and 2002 were not conducted because grasses were not identified to species on those dates; such an analysis would have excluded the majority of the biomass (graminoid) in this community. All analyses were performed with PC-Ord ver. 4.14 (McCune and Medford, 1999).

Once overall floristic differences were tested for, I examined individual species responses using indicator species analysis (Dufrêne and Legendre 1997). This method determines which species are significantly associated with each treatment. These are not *a priori* hypothesis tests, since no predictions are made regarding which species will respond, and in what way. Rather, the purpose of this method is to search for patterns that can be the subject of future investigation. Indicator species analysis uses two relevant pieces of information: the abundance of that species across treatments, and its frequency of occurrence, to produce indicator values for each species by treatment combination thus:

$$A_{ij} = N(\text{individuals})_{ij} / N(\text{individuals})_i$$

$$\text{and } B_{ij} = N(\text{sites})_{ij} / N(\text{sites})_j$$

$$\text{and } \text{IndVal}_{ij} = A_{ij} \times B_{ij} \times 100$$

where $N(\text{individuals})_{ij}$ is the mean abundance of species i in treatment j , $N(\text{individuals})_i$ is the mean abundance of species i across all treatments, $N(\text{sites})_{ij}$ is the number of occurrences of species i in treatment j , and $N(\text{sites})_i$ is the number of plots in that treatment. The significance of the treatment effect is also determined by randomization. This allowed calculation of P values for each species, where a significant P value indicates that the species occurs more often in some treatments than in others. Similar to the MRPP, this test only accommodates one factor at a time, so separate models are presented for each insecticide treatment. Since this method does not support a blocking factor, and most species form a small component of total cover, power of individual tests is likely to be low, increasing the likelihood of Type II errors. However, analyses are conducted on all species, increasing the likelihood of Type I errors. As a compromise, I ran the analyses and recorded all species that rejected the null with a Type I error rate $P < 0.1$ for each species. Of these, only those species that found this result on more than one date were considered significant, unless the resulting P value was less than 0.05; all such results are reported. Indicator species values were calculated on cover and biomass data from each date.

Results

Cover and standing biomass

There were no baseline differences between treatments in canopy cover at the start of the experiment, and total canopy cover was unaffected by either above or below-ground insect suppression during the first year of the insecticide

application. During the following growing season, total percent cover was lower in all plots compared to 12 months prior (Fig. 3.4a, Table 3.1). Canopy cover during 2002 was significantly higher in plots where above-ground insects were suppressed; this pattern appeared to be driven largely by the grasses (Fig. 3.4c, Table 3.1). Light penetration in August 2002 was lower in plots where above-ground insects had been suppressed ($F_{1,27} = 6.62$; $P = 0.0159$). Total species richness was unaffected throughout 2001, but grass species richness was lower in plots sprayed with above-ground insecticide (July and August observations only) and there was a below-ground insecticide by time interaction (Table 3.2; Fig. 3.5c). Total species richness during July and August 2002 was significantly affected by the 3-way interaction of two insecticide treatments and time (Table 3.2; Fig. 3.5a). This pattern was driven by forbs (Table 3.2; Fig. 3.5b); when forbs and grasses were considered separately, forb species richness was higher in plots sprayed with above-ground insecticide in August 2002, with an above-ground insecticide by time interaction, while grasses were unaffected (Fig. 3.5c).

There were no significant differences between treatments in above-ground biomass at any time (Fig. 3.6a, Table 3.3). Above-ground biomass was about 4 times lower in July of 2002 than in July 2001; reflecting the extended drought. Root biomass, the majority of phytomass present in the system, changed little between years and there were no significant treatment effects (Fig. 3.6b, Table 3.4a). During 2001, when root and shoot biomass were harvested at the same time, total plant biomass was also unaffected by insect suppression (Fig. 3.6c, Table 3.4b).

Focal plant response

Insecticide suppression reduced insect damage to focal plants on June 26th and July 12th, but not on August 12th (Fig. 3.7a-c, Table 3.5). The non-significance of the insecticide effect in August is probably due in part to low statistical power, since most plants had died by this time. There was also an insecticide by species interaction on July 12th, suggesting that the insecticide was more effective in reducing insect damage in some species than in others (Table 3.5). In unsprayed plots, plant species had a significant ($F_{5,98} = 2.97$; $P = 0.0154$) effect on the frequency of insect damage on June 26th (Fig. 3.6a). On later dates, the relatively invulnerable species, *Achillea millefolium* and *Cerastium arvense*, had mostly died, which may explain the non-significance of the species effects on July 12th and August 12th (Table 3.6). Focal plant mortality was largely unaffected by insect suppression (Table 3.7). Only *Aster falcatus* was significantly affected by the treatment, with greater ramet mortality in unsprayed plots on July 12th. Neither plant height (Fig. 3.8a-c, Table 3.8) nor leaf count (Fig. 3.9a-c, Table 3.9) were affected by insect suppression. High mortality precluded analysis of effects on biomass for all but two species, *Rosa arkansana*, and *Aster falcatus*. Their biomass was not affected by insect suppression (*Rosa arkansana*: $F_{1,15} = 0.51$ and $P = 0.4860$; *Aster falcatus*: $F_{1,9} = 0.00$ and $P = 0.9805$).

Community composition

The blocked MRPP on the cover data revealed significant effects of the above-ground insecticide treatment in August of 2001 but on no other dates (Table 3.10a). Indicator species analysis of the cover and biomass data revealed sporadic, significant individual species responses, with few species that were systematically affected by any insecticide treatment. Most significant results were associated with the above-ground insecticide. The indicator species in the cover data tended to have greater cover in plots treated with the above-ground insecticide (Table 3.11). In the biomass data (Table 3.12), most significant differences were in plots sprayed with above-ground insecticide, with most species having greater biomass in plots treated with above-ground insecticide (note that graminoid responses were not measured by species). When species were significantly associated with a treatment on more than one sampling date, it was in all cases greater biomass or cover in plots with the above-ground treatment. The grass *Stipa curti-setta* had greater cover in plots with above-ground insect suppression in July of 2001 and 2002. The legume *Oxytropis sericea* had higher biomass in plots with above-ground insect suppression in July of 2001 and 2002, and the legume *Thermopsis rhombifolia* had higher biomass in response to above-ground insect suppression in August 2001, and higher cover in July 2002 (Tables 3.11, 3.12).

Discussion

This study is one of a few to have examined the effects of insects on primary production and community composition, in a mature plant community, at non-outbreak levels. Here, above-ground insects were of little importance to the most basic measures by which ecologists describe plant communities (Kent and Coker, 1992; Sala and Austin, 2000). Primary production and growth of individual plants were all unaffected by insect suppression (Figs. 3.6, 8, and 9). Percent ground cover was increased by insect suppression, but only after a year of sustained insect suppression (Fig. 3.4). These results are consistent with models holding that insects have little effect on ecosystem function (Strong et al., 1984) or plant population dynamics (Crawley, 1989) due to regulation of insect herbivore populations by their natural enemies (Hairston et al., 1960; Marquis and Whelan, 1994; Karhu, 1998; Moran and Hurd, 1998), or because most plants are of low quality as food (McNeill and Southwood, 1973; Janzen, 1988; Hartley and Jones, 1997). I now turn to some of the specific results and their interpretation.

Primary production and cover

The 15% greater cover in plots with above-ground insect suppression suggests a positive growth response of the whole plant community to insect suppression. Primary production, however, was only 10% greater in plots with above-ground insect suppression, and this was not a significant difference (Fig. 3.6a). The significance of this disparity is unclear, but it is likely due to the

structures that account for the difference in cover (leaves) having a relatively small effect on biomass.

A finding of no effect of insects on primary production is in contrast to findings in communities where an outbreak was taking place (Carson and Root, 1999; 2000), and frequent demonstrations of insect depression of production in ryegrass-dominated sown pasture (Henderson and Clements, 1977; Clements et al., 1982). However, in self-sown communities where effects of insects at non-outbreak levels on community structure have been measured, primary production has rarely been measured (McBrien et al., 1983; Hendrix et al., 1988; Brown and Gange, 1992). In that sense, this result, though predicted by long-standing theory (Hairston et al., 1960; Strong et al., 1984; Crawley 1989; Hartley and Jones 1997) is a novel one. I suggest that the view that grasshoppers alone have a pronounced (20%) negative effect on primary production in North American grasslands (Hewitt and Onsager, 1983) may be more reflective of the history of rangeland entomology, which has placed an emphasis on outbreaks and insect densities at which control becomes profitable (Watts et al., 1982). Significant effects of insects on above-ground primary production are more likely to appear in future years of this type of study, as we found during our meta-analysis of insect effects on primary production (Coupe and Cahill, unpublished). However, the magnitude of the effect we have observed on primary production is small in relation to what has been predicted by other authors.

Similar to above-ground production, root biomass was unaffected by insect suppression (Fig. 3.6b) and there were no consistent trends in root biomass

as a function of treatment. This is significant because root biomass formed the majority of plant biomass in this system (Fig. 3.6). A lack of an effect of insects on root biomass suggests that overall, insects had a minimal effect on community function, regardless of their effect on cover. However, a disadvantage of the method used to estimate root biomass in this study is that it is unable to distinguish between living and dead roots. If dead roots form a large component of the root biomass, then the effects of insects on root growth must be measured using different methods. In fact, a companion study during 2002 showed that buried dead root samples in were highly recalcitrant, losing very little of their mass through the course of the year, presumably in part due to the drought. Their rate of mass loss was unaffected by insect suppression (Coupe and Cahill, unpublished data). A better method of evaluating the effects of insects on root growth would be one not relying upon such static measures. In particular, minirhizotrons have been placed in the plots for a companion study, and there is early evidence that above-ground insect suppression alters root turnover (Cahill, pers. comm.).

Species richness

The significantly higher forb species richness in plots sprayed with above-ground insecticide in August 2002 is noteworthy. Species richness in general declined between July and August 2002, but there was less of a decline in plots without above-ground insects. From this result alone, it is unclear whether this occurred due to greater seedling or ramet recruitment, or reduced ramet mortality.

Significant effects of insect herbivory on seedling mortality have been demonstrated in early successional situations (Brown and Gange 1989), but since species richness was unaffected in July, and seedlings were very rare in the soil cores in 2002 (pers. obs.), this is the least likely scenario. Therefore, it seems most likely that the greater species richness was due either to increased recruitment of new ramets of established plants, or due to lower overall ramet mortality. Based upon the high ramet mortality and low primary production (both due to the drought), and the fact that a net reduction in species richness occurred between July and August, the latter explanation seems most likely. However, this conclusion is not compatible with the focal plant experiment, in which mortality of 5 of the 6 most common forbs was unaffected by insect suppression. Low statistical power is the most likely explanation; mortality was so high by this time that cover measures (which can detect several plants) were more likely to detect the effect than were repeated observations of individual plants.

A greater plant species richness in response to insect suppression contrasts with results of insect suppression in another mature plant community: the highly productive old field examined by Carson and Root (2000). Their system was dominated by the goldenrod *Solidago altissima*, a tall perennial forb which competes asymmetrically for light, maintaining low species richness when it shades subdominant and understory plants. Such findings are consistent with Crawley's (1989b) model in which herbivory causes a reduction of the intensity of competition between plants when growth is strongly light-limited. If rare

species suffer less from herbivory, and palatable species are not poorer competitors, then herbivory can increase species diversity (Pacala and Crawley, 1992). In this system, there was no evidence for such a phenomenon. During 2002, light competition had no effect on seedling establishment (Cahill, in press) so there was no light competition from which plants could be released. Instead, these results are compatible with Olff and Ritchie's (1998) model of small herbivore effects on plant diversity in dry, infertile grasslands. They hypothesized that herbivores would select rare, palatable plant species and that any effect on plant competition would be unlikely to trigger plant coexistence. Small herbivores are expected to have a small, negative effect on plant species diversity without dramatic effects on community structure. Selective herbivory is not necessary to generate this pattern; random removal of plants from unsprayed plots could also lead to decreases in species richness at the scale observed in this study. However, the fact that forb richness decreased while grass richness was unaltered suggests that some herbivore selectivity is involved. This is supported by the significantly lower cover and biomass of the legume *Thermopsis rhombifolia* Nutt. (Richards) in plots with above-ground insects; we have found in a companion study that this species is extremely susceptible to insect herbivory (Shore et al., unpublished). Additionally, the common forb *Solidago missouriensis* had higher cover in plots sprayed with above-ground insecticide in August 2002 (Table 3.11), and this species was frequently attacked in the focal plant study (Fig. 3.6).

In addition to spatial variation, temporal variation in productivity may also interact with the insect herbivory to alter plant species richness. If release from light competition by insect herbivory can promote plant diversity in this system, then the effects of insects on species richness are expected to be negative in low productivity years, and positive in years with high productivity and resulting greater light competition. The other significant effect on plant species richness was the greater graminoid species richness in plots not sprayed with above-ground insecticide in the summer of 2001. In other words, this is the opposite result: higher species richness in the presence of herbivory rather than in its absence. This is support for the hypothesis that an interaction exists between temporal variation in productivity, and the herbivore-mediated changes in species richness. However, this necessitates disappearance of mature (identifiable) grass tussocks in response to herbivore suppression during the field season of the initiation of the experiment. Since the ease with which grasses could be identified changed through the first field season, I suggest that the latter interpretation lacks the ecological realism of my interpretation of the change in forb species richness during the second field season.

Community composition

The combination of the MRBPs and indicator species analyses provides greater sensitivity to conclusions regarding the effects of insects on community composition. Although no gross measures of community structure and function were affected during the first year, floristic composition, as measured by cover,

was significantly altered by insecticide application in August 2001. It is significant that the grass shown, *Stipa curtisetta*, which accounted for much of the increase in cover in sprayed plots in 2002, also had significantly greater cover at the same time in 2001, suggesting that the effects of insect herbivory on cover had begun in 2001 and were cumulative. Two of the species that consistently exhibited positive responses to the above-ground insect suppression, *Thermopsis rhombifolia*, and *Oxytropis sericea* Nutt., are legumes (Tables 3.11, 3.12). Legumes are preferentially consumed by herbivores, apparently due to their high nitrogen content (Hulme, 1995; Ritchie and Tilman, 1996), and nitrogen is a limiting factor to insect herbivore growth (McNeill and Southwood, 1978). However, the presence of significant indicator species is not necessary for a significant MRBP. The MRBP in August 2001 remained significant when the two significant indicator species were removed from the data (Observed delta = 14.50; expected delta = 15.11; $P = 0.0404$), suggesting that incremental changes in relative species abundances had occurred in response to insect suppression.

Observations of insect damage in the focal plant experiment are also suggestive of a potential for changes in community composition as a result of insect suppression as this experiment progresses. Insect herbivory was species-specific, with little chewing damage on two of the species (*Achillea millefolium* and *Cerastium arvense*), and frequent damage on the remaining four. Although the intensity of the attack was low for most species (rarely greater than 5%), if the direct effects of herbivore damage to plant growth can affect community

structure, then the undamaged species may become more dominant in the sprayed plots as this experiment progresses.

The role of drought

The decline in cover and standing biomass from 2001 to 2002 reflects the dramatic, direct effects of the continuing drought on plant growth. However, drought may also affect plant growth indirectly by inducing outbreaks of insect herbivores (Mattson and Haack, 1987). Could the significant effects of insect herbivory in 2002 be due to an interaction with the drought? Interactions between water stress and the impact of herbivory may be negative if vigorous plants have greater food quality (Price, 1991; Schowalter et al., 1999) or synergistic if stressed plants have greater food quality (Louda and Rodman, 1996; Schowalter et al., 1999). If the effects of drought on food quality in this system are positive then the drought may have been a factor in the observation of significant effects during the 2002 drought. The available evidence suggests that water stress improves food quality for piercing insects such as homopterans, but reduces food quality for chewers, such as grasshoppers and lepidopterans (Schowalter et al., 1999). Since grasshopper numbers and apparent biomass far exceeded that of homopterans in the second year of the drought, it is likely that the insects responsible for most above-ground insect herbivory were actually experiencing lower food quality than usual. However, grasshopper populations may also be affected by drought through mechanisms other than food quality, such as improved reproductive conditions following warm years (Joern and Gaines,

1990). Positive correlations between the previous years' heat/precipitation ratio, and grasshopper abundance have been repeatedly demonstrated in agricultural regions of Alberta, Saskatchewan, and the northwestern continental United States (Gage and Mukerji, 1977; Johnson and Worobec, 1988; Capinera and Horton, 1989). If improved reproductive conditions result from hot, dry weather, then successive warm years as seen in this study could lead to acute effects of insect herbivores, particularly grasshoppers, on plant growth, implying that the effects seen in the second year of this study were actually more intense than average.

2003 is the third year of the study and it has been a non-drought year. Cover, above-ground biomass, and plant species richness have been considerably higher, in part due to recruitment of seedlings of some species not seen in prior years (Coupe, unpublished data). During early succession, with its extensive seedling recruitment, insects have been shown to have pronounced effects on community structure in other systems (Brown and Gange, 1992; Carson and Root 1999). We suggest that the seedling recruitment following drought as seen in this study has presented another opportunity for insect-induced shifts in community structure. Further analysis of the results from 2003 will allow examination of this hypothesis.

Summary of results

In this system, insect herbivory reduces vegetation cover and forb species richness, causes chewing damage that is species specific, and alters cover and biomass of many common forbs and grasses. However, the effects on cover and

species richness only began following two years of sustained insect exclusion. Furthermore, unlike other grassland and forb-dominated communities, primary production was unaffected by insect suppression. In contrast, the sustained drought had dramatic effects on plant community structure, reiterating the known importance of resource supply in this system. However, the finding that insects suppress plant species richness and cover during a drought year is in agreement with models suggesting that there is an interaction between resource supply and effects of insect herbivory on plant community structure.

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Table 3.1. Repeated measures analysis of plant cover during the summers of 2001 and 2002. The following codes are used: "AGI" refers to the above-ground insecticide, "BGI" refers to the below-ground insecticide, the factor "time" is the sampling date effect, and "Bk" refers to the blocking factor (random). Significant results are shown in bold.

Summer 2001: total cover					Summer 2002: total cover				
Fixed effects	Num df	Den df	F	P	Fixed effects	Num df	Den df	F	P
AGI	1	9	0.02	0.8887	AGI	1	81	15.27	0.0002
BGI	1	18	0.03	0.8558	BGI	1	18	0.00	0.9665
AGI*BGI	1	81	0.05	0.8318	AGI*BGI	1	81	2.25	0.1379
Time	2	81	158.69	< 0.0001	Time	2	18	103.00	< 0.0001
AGI*time	2	81	0.26	0.7699	AGI*time	2	81	4.27	0.0172
BGI*time	2	81	0.19	0.8302	BGI*time	2	81	0.64	0.5304
3-way interaction	2	81	0.51	0.6002	3-way interaction	2	81	0.68	0.5087
Random effects retained: Bk*BGI, Bk*AGI, Bk*AGI*BGI*time					Random effects retained: Bk, Bk*time, Bk*AGI*BGI*time				

Summer 2001: forb cover					Summer 2002: forb cover				
Fixed effects	Num df	Den df	F	P	Fixed effects	Num df	Den df	F	P
AGI	1	36	0.00	0.9493	AGI	1	36	1.65	0.2071
BGI	1	36	0.41	0.5276	BGI	1	36	0.03	0.8725
AGI*BGI	1	36	0.08	0.7762	AGI*BGI	1	36	1.30	0.2617
Time	2	72	57.50	< 0.0001	Time	2	36	28.85	< 0.0001
AGI*time	2	72	0.15	0.8647	AGI*time	2	36	1.33	0.2776
BGI*time	2	72	0.91	0.4085	BGI*time	2	36	0.57	0.5717
3-way interaction	2	72	1.09	0.3426	3-way interaction	2	36	1.25	0.2983
Random effect retained: Bk*AGI*BGI					Random effects retained: Bk*AGI*BGI, Bk*time, Bk*AGI*BGI*time				

Summer 2001: grass cover					Summer 2002: grass cover				
Fixed effects	Num df	Den df	F	P	Fixed effects	Num df	Den df	F	P
AGI	1	90	0.45	0.5054	AGI	1	81	14.16	0.0003
BGI	1	9	0.32	0.5858	BGI	1	81	0.35	0.5539
AGI*BGI	1	90	0.00	0.9848	AGI*BGI	1	81	2.25	0.1376
Time	2	90	248.68	< 0.0001	Time	2	18	95.90	< 0.0001
AGI*time	2	90	1.40	0.2510	AGI*time	2	81	5.03	0.0087
BGI*time	2	90	0.21	0.8075	BGI*time	2	81	0.34	0.7145
3-way interaction	2	90	0.10	0.9038	3-way interaction	2	81	0.97	0.3851
Random effects retained: Bk, Bk*BGI, Bk*AGI*BGI*time					Random effects retained: Bk, Bk*time, Bk*AGI*BGI*time				

Table 3.2. Repeated measures analysis of species richness measured from cover during the summers of 2001 and 2002. The codes and symbols used are the same as used in Table 3.1.

Summer 2001: total richness					Summer 2002: total richness				
Fixed effects	Num df	Den df	F	P	Fixed effects	Num df	Den df	F	P
AGI	1	18	1.83	0.1932	AGI	1	18	2.82	0.1104
BGI	1	18	0.00	0.9710	BGI	1	54	1.17	0.2851
AGI*BGI	1	18	0.11	0.7436	AGI*BGI	1	54	0.06	0.8113
Time	1	9	1.45	0.2590	Time	1	54	76.68	<0.0001
AGI*time	1	27	0.01	0.9389	AGI*time	1	54	0.52	0.4748
BGI*time	1	27	12.11	0.0017	BGI*time	1	54	1.74	0.1926
3-way interaction	1	27	0.01	0.9389	3-way interaction	1	54	4.66	0.0353

Random effects retained: Bk*AGI, Bk*time, Bk*AGI*BGI Random effects retained: Bk*AGI, Bk*AGI*BGI*time

Summer 2001: forb richness					Summer 2002: forb richness				
Fixed effects	Num df	Den df	F	P	Fixed effects	Num df	Den df	F	P
AGI	1	36	0.37	0.5468	AGI	1	36	0.59	0.4461
BGI	1	36	0.08	0.7728	BGI	1	36	2.14	0.1520
AGI*BGI	1	36	0.59	0.4481	AGI*BGI	1	36	0.02	0.8784
Time	2	72	20.23	<0.0001	Time	2	72	65.23	<0.0001
AGI*time	2	72	0.15	0.8645	AGI*time	2	72	6.06	0.0037
BGI*time	2	72	1.71	0.1887	BGI*time	2	72	0.73	0.4874
3-way interaction	2	72	0.26	0.7686	3-way interaction	2	72	2.95	0.0589

Random effect retained: Bk*AGI*BGI Random effects retained: Bk*AGI*BGI, Bk*AGI*BGI*time

Summer 2001: grass richness					Summer 2002: grass richness				
Fixed effects	Num df	Den df	F	P	Fixed effects	Num df	Den df	F	P
AGI	1	36	4.19	0.0479	AGI	1	72	0.40	0.5276
BGI	1	36	0.15	0.7033	BGI	1	72	0.40	0.5276
AGI*BGI	1	36	1.98	0.1678	AGI*BGI	1	72	0.04	0.8330
Time	1	36	0.00	1.0000	Time	2	72	1.61	0.2083
AGI*time	1	36	0.15	0.7029	AGI*time	2	72	0.72	0.4001
BGI*time	1	36	4.47	0.0414	BGI*time	2	72	0.72	0.4001
3-way interaction	1	36	0.04	0.8486	3-way interaction	2	72	0.72	0.4001

Random effect retained: Bk*AGI*BGI Random effect retained: Bk*AGI*BGI*time

Table 3.3. Repeated measures analysis of total above-ground biomass, forb biomass, and graminoid biomass during the summers of 2001 and 2002. Only one above-ground biomass measurement was taken during 2002, due to the drought. Codes are the same as those used in Table 3.1.

Summer 2001: total biomass					July 2002: total biomass				
Fixed effects	Num df	Den df	F	P	Fixed effects	Num df	Den df	F	P
AGI	1	36	0.20	0.6556	AGI	1	36	0.40	0.5303
BGI	1	36	0.09	0.7655	BGI	1	36	0.23	0.6378
AGI*BGI	1	36	0.22	0.6413	AGI*BGI	1	36	0.56	0.4601
Time	2	36	208.61	< 0.0001					
AGI*time	2	36	0.30	0.7401					
BGI*time	2	36	0.00	0.9951					
3-way interaction	2	36	0.26	0.7718					
Random effects retained: Bk*AGI*BGI, Bk*BGI*time, Bk*AGI*BGI*time					Random effect retained: Bk*AGI*BGI				

Summer 2001: forb biomass					July 2002: forb biomass				
Fixed effects	Num df	Den df	F	P	Fixed effects	Num df	Den df	F	P
AGI	1	9	0.40	0.5438	AGI	1	36	0.28	0.6012
BGI	1	1	0.33	0.5753	BGI	1	36	0.39	0.5370
AGI*BGI	1	45	0.00	0.9555	AGI*BGI	1	36	0.79	0.3790
Time	2	36	62.09	< 0.0001					
AGI*time	2	45	0.96	0.3894					
BGI*time	2	36	0.11	0.9000					
3-way interaction	2	45	0.02	0.9809					
Random effects retained: Bk*BGI, Bk*AGI, Bk*BGI*time					Random effect retained: Bk*AGI*BGI				

Summer 2001: graminoid biomass					July 2002: graminoid biomass				
Fixed effects	Num df	Den df	F	P	Fixed effects	Num df	Den df	F	P
AGI	1	27	0.01	0.9275	AGI	1	18	0.60	0.4479
BGI	1	27	0.02	0.8951	BGI	1	18	0.05	0.8178
AGI*BGI	1	27	0.38	0.5412	AGI*BGI	1	18	0.55	0.4680
time	2	54	96.33	< 0.0001					
AGI*time	2	54	1.17	0.3189					
BGI*time	2	54	0.04	0.9575					
3-way interaction	2	54	0.34	0.7152					
Random effects retained: Bk*time, Bk*AGI*BGI, Bk*AGI*BGI*time					Random effect retained: Bk*BGI				

Table 3.4. Repeated measures analysis of root biomass during the summers of 2001 and 2002, and total biomass during the summer of 2001. Codes are the same as used in Table 3.1.

Summer 2001: root biomass					May 2002: root biomass				
Fixed effects	Num df	Den df	F	P	Fixed effects	Num df	Den df	F	P
AGI	1	94	0.01	0.9216	AGI	1	36	1.41	0.2432
BGI	1	94	0.31	0.5801	BGI	1	36	0.49	0.4885
AGI*BGI	1	94	1.50	0.2231	AGI*BGI	1	36	1.42	0.2413
Time	2	94	0.05	0.9525					
AGI*time	2	94	1.10	0.3385					
BGI*time	2	94	0.75	0.4768					
3-way interaction	2	94	0.73	0.4854					
Random effect retained: Block					Random effect retained: Block*AGI*BGI				
Summer 2001: total biomass									
Fixed effects	Num df	Den df	F	P					
AGI	1	103	0.00	0.9629					
BGI	1	103	0.25	0.6165					
AGI*BGI	1	103	1.57	0.2136					
Time	2	103	1.31	0.2745					
AGI*time	2	103	1.09	0.3390					
BGI*time	2	103	0.70	0.5005					
3-way interaction	2	103	0.67	0.5140					
Random effect retained: 4-way interaction									

Table 3.5. Effects of species identity and insecticide treatment on the frequency of insect damage on *Comandra umbellata*, *Aster falcatus*, *Rosa arkansana*, and *Solidago missouriensis* on three dates. Codes are the same as those used in Table 3.1. As the focal plant experiment was not conducted in plots treated with below-ground insecticide, in all cases "insecticide" refers to the above-ground insecticide effect. By August 12th, few plants survived, and these were predominantly *Rosa arkansana* and *Aster falcatus*, so the statistical test is likely to have considerably less power.

Date	Species		Insecticide		Insecticide*species	
	F _{df}	P	F _{df}	P	F _{df}	P
June 26th	F _{3,138} = 1.08	0.3591	F _{1,138} = 18.62	< 0.0001	F _{3,138} = 1.83	0.1452
July 12th	F _{3,105} = 1.05	0.3738	F _{1,105} = 12.02	0.0008	F _{3,105} = 2.81	0.0433
August 12th	F _{3,38} = 0.32	0.8125	F _{1,38} = 0.00	0.9997	F _{3,38} = 0.07	0.9291

Table 3.6. Effects of species identity on frequency of insect damage to all 6 species of focal plants on three dates. Codes are the same as used in Table 3.1.

Date	Species	
	F	P
June 26th	$F_{5,98} = 2.97$	0.0154
July 12th	$F_{5,67} = 0.82$	0.5410
August 12th	$F_{4,18} = 0.44$	0.7769

Table 3.7. Effects of insecticide treatment on mortality of all 6 species of focal plants on 3 dates. High mortality precluded meaningful tests of the insecticide effect on August 12th for all but 2 species.

Species	Date	Insecticide		Random factor
		F	P	Block covariance parameter
<i>Achillea millefolium</i>				
	June 26th	F _{1,45} = 0.17	0.6863	0.00
	July 12th	F _{1,45} = 0.00	0.9681	0.01
<i>Aster falcatus</i>				
	June 26th	F _{2,29} = 0.21	1.0000	0.00
	July 12th	F _{1,29} = 4.32	0.0466	0.00
	August 12th	F _{1,29} = 0.13	0.7215	0.00
<i>Cerastium arvense</i>				
	June 26th	F _{1,55} = 2.30	0.1351	0.00
	July 12th	F _{1,55} = 0.47	0.4976	0.00
<i>Commandra umbellata</i>				
	June 26th	F _{1,48} = 0.01	0.9277	0.08
	July 12th	F _{1,48} = 0.17	0.6862	0.05
<i>Rosa arkansana</i>				
	June 26th	F _{1,48} = 0.00	0.9977	0.00
	July 12th	F _{1,48} = 0.88	0.3523	0.00
	August 12th	F _{1,48} = 0.17	0.6778	0.05
<i>Solidago missouriensis</i>				
	June 26th	F _{1,41} = 0.32	0.5752	0.00
	July 12th	F _{1,41} = 2.09	0.1556	0.00
	August 12th	F _{1,41} = 2.65	0.1113	0.02

Table 3.8. Effects of insecticide treatment on height of all 6 species of focal plants on 3 dates.

Species	Date	Insecticide		Random effects retained
		F	P	
<i>Achillea millefolium</i>				
	May 25th	F _{1,46} = 0.05	0.8223	Plant (AGI*block)
	June 26th	F _{1,36} = 0.34	0.5659	Plant (AGI*block)
<i>Aster falcatus</i>				
	May 25th	F _{1,22} = 0.60	0.4453	Block, Plant (AGI*block)
	June 26th	F _{1,29} = 0.01	0.9129	Plant (AGI*block)
	August 12th	F _{1,3} = 0.77	0.4441	Block
<i>Cerastium arvense</i>				
	May 29th	F _{1,56} = 0.13	0.7236	Plant (AGI*block)
	June 26th	F _{1,31} = 0.00	0.9474	Plant (AGI*block)
<i>Commandra umbellata</i>				
	May 25th	F _{1,49} = 1.32	0.2569	Plant (AGI*block)
	June 26th	F _{1,35} = 0.50	0.4828	Plant (AGI*block)
<i>Rosa arkansana</i>				
	May 25th	F _{1,49} = 1.72	0.1961	Plant (AGI*block)
	June 26th	F _{1,46} = 1.49	0.2280	Plant (AGI*block)
	August 12th	F _{1,15} = 0.34	0.5660	AGI*block
<i>Solidago missouriensis</i>				
	May 25th	F _{1,33} = 0.06	0.8085	Block, Plant (AGI*block)
	June 26th	F _{1,28} = 1.90	0.1790	Block, Plant (AGI*block)

Table 3.9. Effects of insecticide treatment on leaf count of all 6 species of focal plants on 3 dates.

Species	Date	Insecticide		Random effects retained
		F	P	
<i>Achillea millefolium</i>				
	May 25th	F _{1,46} = 0.00	0.9630	Plant (AGI*block)
	June 26th	F _{1,27} = 0.02	0.8790	Block
<i>Aster falcatus</i>				
	May 25th	F _{1,30} = 3.17	0.0850	Plant (AGI*block)
	June 26th	F _{1,12} = 0.04	0.8376	Plant (AGI*block), AGI*block
	August 12th	F _{1,9} = 2.02	0.1886	Plant (AGI*block)
<i>Cerastium arvense</i>				
	May 29th	F _{1,56} = 0.52	0.4758	Plant (AGI*block)
	June 26th	F _{1,31} = 0.99	0.3285	Plant (AGI*block)
<i>Commandra umbellata</i>				
	May 25th	F _{1,49} = 0.02	0.8890	Plant (AGI*block)
	June 26th	F _{1,35} = 0.65	0.4261	Plant (AGI*block)
<i>Rosa arkansana</i>				
	May 25th	F _{1,49} = 2.97	0.0913	Plant (AGI*block)
	June 26th	F _{1,46} = 0.41	0.5245	Plant (AGI*block)
	August 12th	F _{1,32} = 0.49	0.4882	Plant (AGI*block)
<i>Solidago missouriensis</i>				
	May 25th	F _{1,42} = 0.76	0.3885	Plant (AGI*block)
	June 26th	F _{1,37} = 2.07	0.1585	Plant (AGI*block)

Table 3.10. Separate results of above- and below-ground insecticide treatments on species composition and relative dominance of the cover data of July and August of both years, using the Blocked Multiple Response Permutation Procedure (MRBP).

Date	Above-ground insecticide effect			Below-ground insecticide effect		
	Observed delta	Expected delta	P	Observed delta	Expected delta	P
July 2nd, 2001	14.4761	14.8290	0.0675	12.9904	13.3256	0.0804
August 19th, 2001	14.9550	15.6002	0.0319	14.0549	14.4474	0.0665
July 11th, 2002	10.6498	10.7349	0.3188	11.3169	11.4825	0.2618
August 12th, 2002	9.1025	9.4027	0.1410	11.4097	11.5750	0.2346

Table 3.11. Indicator species analyses for the cover data on 6 sampling dates. Indicator values are derived from the actual data, while the randomized indicator value is derived from 2000 random permutations of the cover data. Indicator values followed by a "(+)" indicate species that had greater cover in plots with that insecticide treatment; indicator values followed by a "(-)" indicate species that had lower cover in plots with that treatment.

Date	Species	Above-ground insecticide effect			Below-ground insecticide effect		
		Indicator value	Randomized Indicator value	P	Indicator value	Randomized Indicator value	P
May 17th, 2001	no significant responses						
July 2nd, 2001	<i>Stipa curtisetta</i>	58.1 (+)	52.7	0.0175	56.1 (-)	52.7	0.0780
August 19th, 2001	<i>Agropyron</i> spp. 1	57.7 (-)	44.1	0.0390	52.9 (-)	44.1	0.0905
	<i>Agropyron</i> spp. 2	37.6 (-)	18.4	0.0150			
	<i>Solidago missouriensis</i>				56.8 (+)	48.9	0.0830
May 10th, 2002	<i>Comandra umbellata</i> <i>Rosa arkansana</i>	41.7 (+)	27.3	0.0310	57.6 (-)	47.4	0.0655
July 11th, 2002	<i>Stipa curtisetta</i>	59.6 (+)	48.4	0.0490			
	<i>Thermopsis rhombifolia</i> <i>Rosa arkansana</i>	31.2 (+)	21.6	0.0950	56.7 (-)	48.1	0.0795
August 12th, 2002	<i>Solidago missouriensis</i>	48.9 (+)	31.8	0.0190			
	<i>Agropyron</i> spp. 3	36.4 (+)	23.2	0.0445			

Table 3.12. Indicator species analyses for the biomass data on 4 sampling dates. Variable names and codes are identical to those used in Table 3.11.

Date	Species	Above-ground insecticide effect			Below-ground insecticide effect		
		Indicator value	Randomized Indicator value	P	Indicator value	Randomized Indicator value	P
May 4th, 2001 (pre-treatment)	<i>Astragalus agrestis</i> <i>Rosa arkansana</i>	32.3 (+)	18.3	0.0245	61.1 (-)	49.5	0.0375
July 9 th , 2001	<i>Oxytropis sericea</i> <i>Erigeron philadelphicus</i> <i>Cerastium arvense</i>	34 (+)	23.5	0.0730	48.0 (+) 57.8 (+)	32.9 49.3	0.0370 0.0765
August 23rd, 2001	<i>Solidago missouriensis</i> <i>Thermopsis rhombifolia</i>	63.2 (-) 22.5 (+)	50.5 13.5	0.0275 0.0750			
July 13th, 2002	<i>Oxytropis sericea</i> <i>Symphoricarpos occidentalis</i> <i>Cerastium arvense</i>	30.6 (+) 27.6 (+)	20.3 16.4	0.0960 0.0425	55.6 (+)	42.4	0.0780

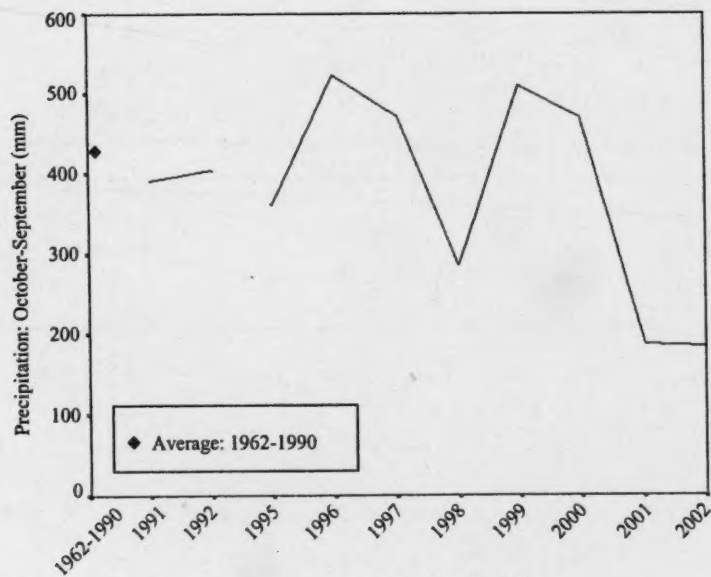


Fig. 3.1. Precipitation records from October to September at Kinsella townsite: 1962-2002. Note that years 1962-1990 are presented as a single average value.

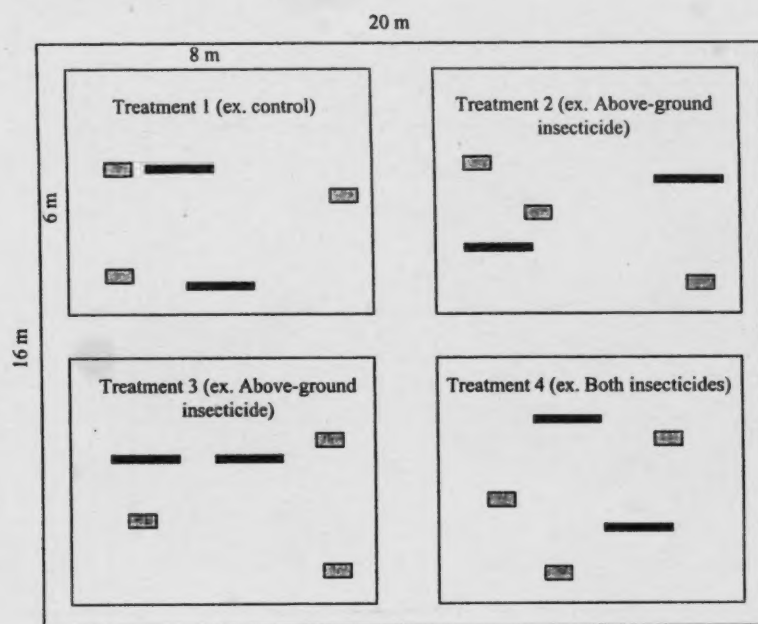


Fig. 3.2. A schematic of a study block with block dimensions and sampling protocol for each harvest. The permanent sampling plots () were 20 x 50 cm and the destructive sampling plots () were 10 x 100 cm. Note that treatment positions were randomized so this is just one possible configuration.

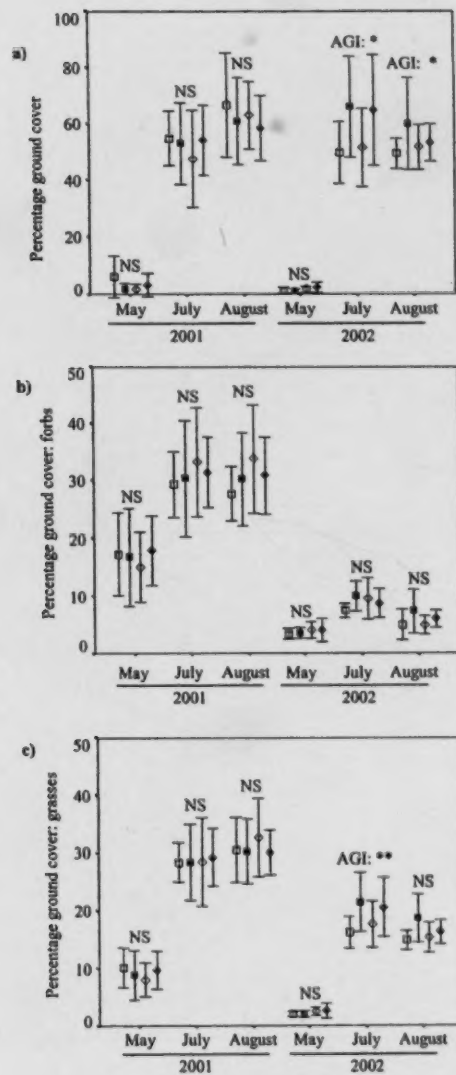


Fig. 3.3. Sweep net counts of a) homopterans, and b) orthopterans, under 4 insecticide treatments. Error bars indicate 95% confidence intervals. The symbols used in the figure legend denote insecticide treatments and are used throughout this paper. The symbols above or below the sets of bars indicate

statistical significance, where "NS" means $P > 0.05$, for all treatments and interactions, and "AGI", "BGI" and "AGI*BGI" indicate significant effects of the above-ground insecticide, the below-ground insecticide, and their interaction, respectively. Significance levels are indicated by asterisks in the following fashion: "*" means $P < 0.05$, "***" means $P < 0.01$, "****" means $P < 0.001$, and "*****" means $P < 0.0001$.

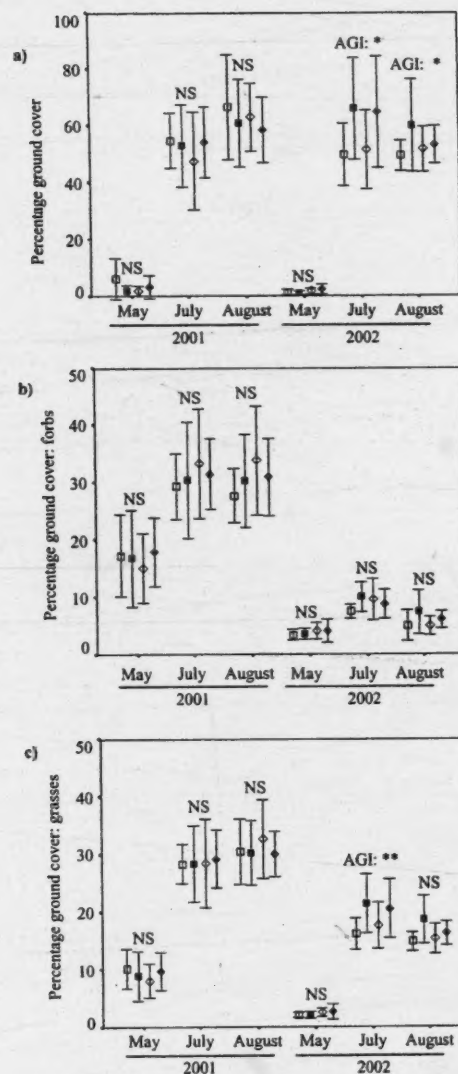


Fig. 3.4. Cover of a) all vegetation, b) all forbs, and c) all grasses, in 4 insecticide treatments during the summers of 2001 and 2002. Error bars indicate 95% confidence intervals. The first observations (May 2001) were made shortly after the beginning of the manipulation when insect densities were very low; thus this can be considered baseline information.

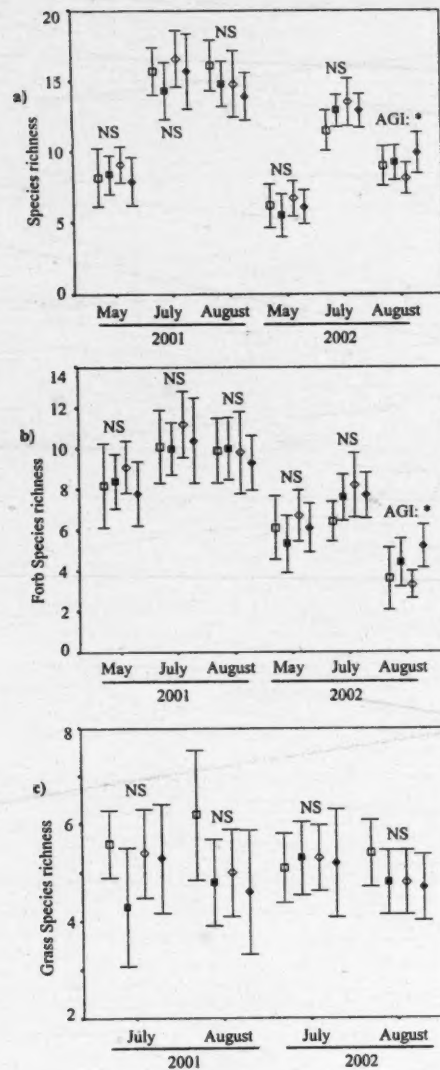


Fig. 3.5. Species richness from cover data of a) all vegetation, b) forbs only, and c) grasses only, in 4 insecticide treatments, during the summers of 2001 and 2002. Error bars indicate 95% confidence intervals.

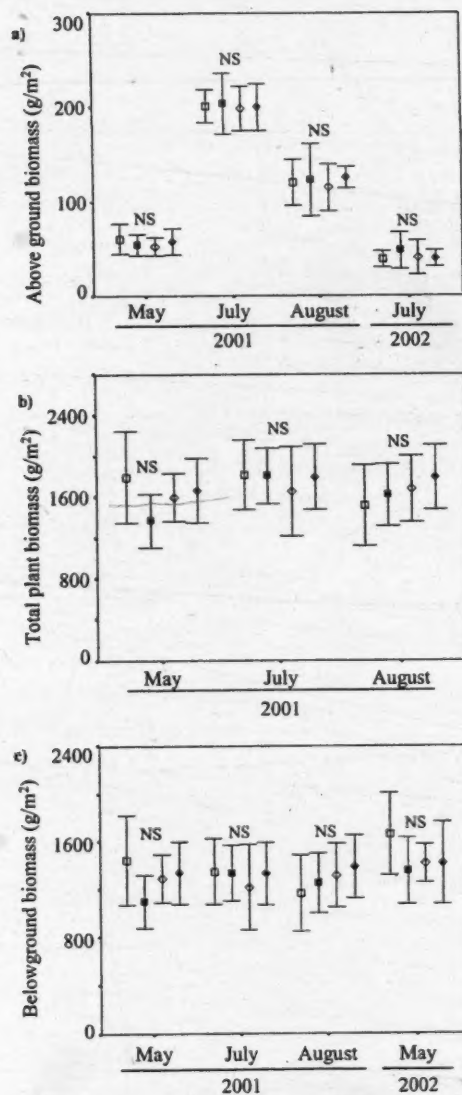


Fig. 3.6. Plant biomass of a) shoots, and b) roots, in 4 insecticide treatments during the summers of 2001 and 2002. Error bars indicate 95% confidence intervals. The first observations (May 2001) were made prior to the beginning of the manipulation.

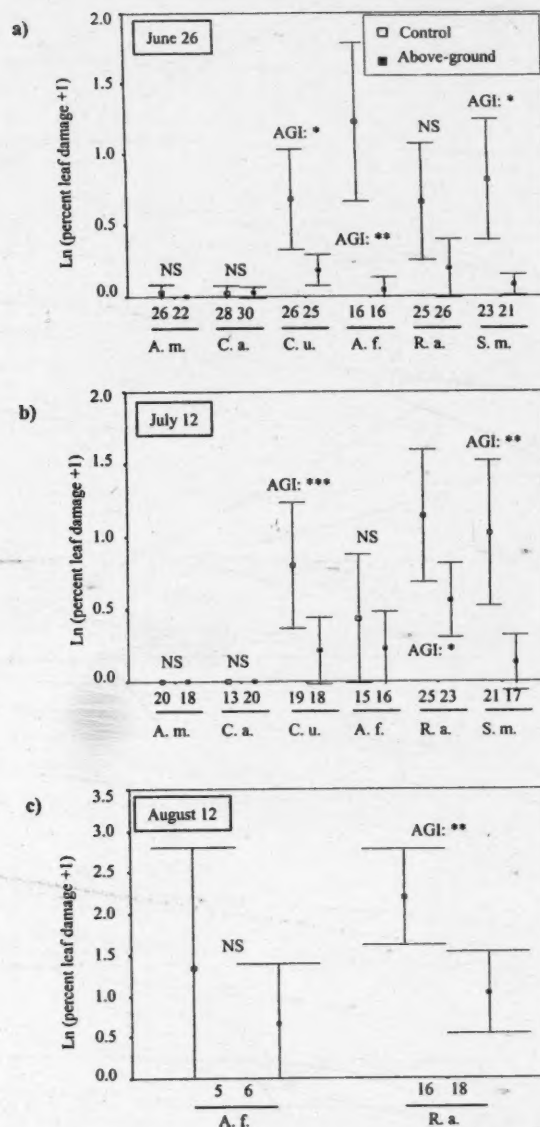


Fig. 3.7. Log_e-transformed percent insect damage to leaves of 6 species of focal plants by chewing insects, in plots sprayed with, and without above-ground insecticide during the summer of 2002. Results are shown from a) June 26th, b) July 12th, and c) August 12th. Error bars indicate 95% confidence intervals. Since focal plants were located in just two treatments, the legend used for the focal plant

experiment is a truncated version of the one used to present results of the community response experiment. For all focal plant results, two letter codes refer to the species' name, where "A.m" is *Achillea millefolium*, "C.a." is *Cerastium arvense*, "C.u." is *Comandra umbellata*, "A.f." is *Aster falcatus*, "R.a." is *Rosa arkansana*, and "S.m." is *Solidago missouriensis*. Figures above each species code are sample sizes. Note that sample sizes change through the season due to plant mortality.

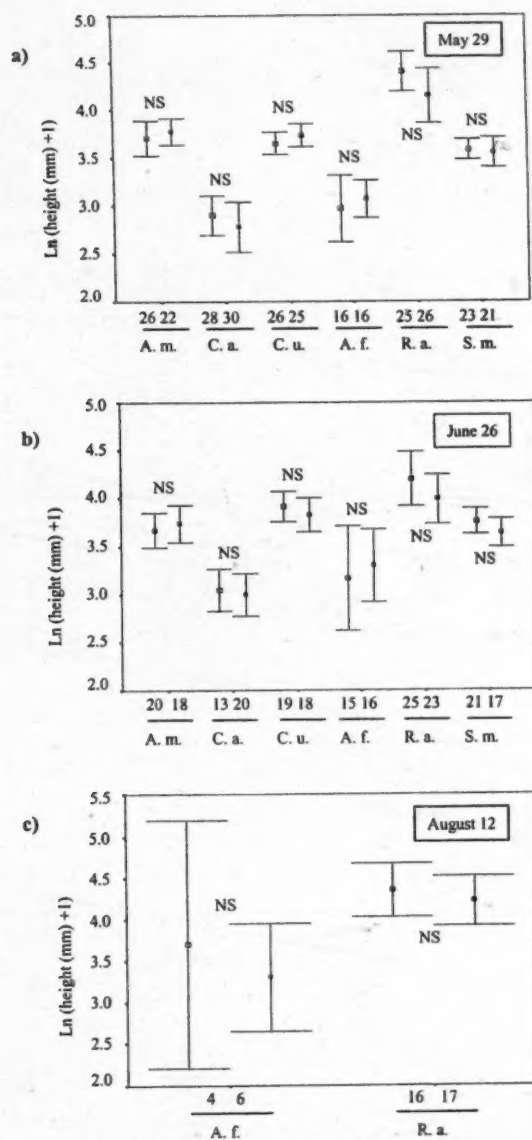


Fig. 3.8. Log_e-transformed height of individual ramets of 6 species of focal plants, in plots sprayed with and without above-ground insecticide during the summer of 2002. Results are shown from a) May 25th, b) June 26th, and c) August 12th. Error bars indicate 95% confidence intervals.

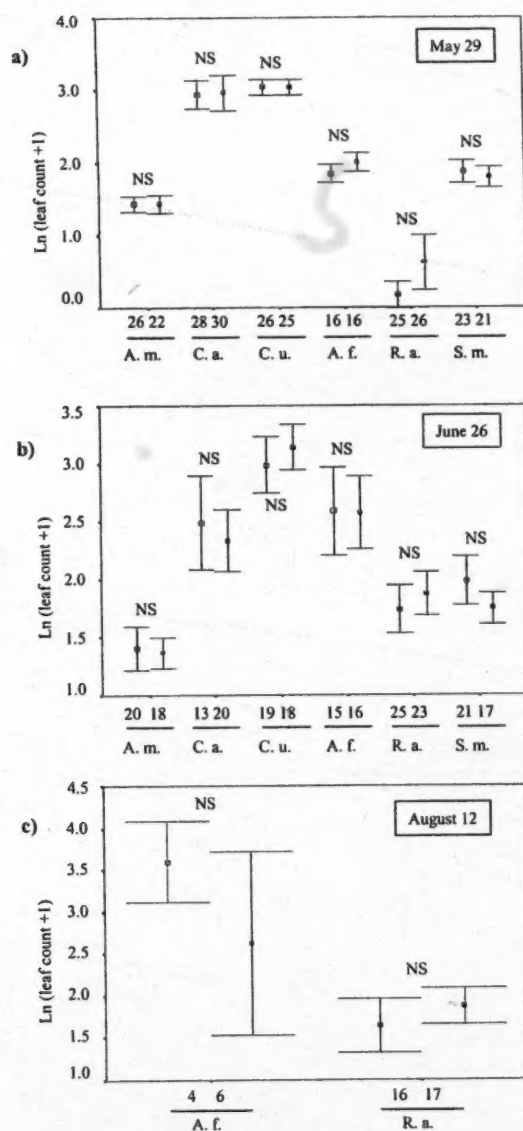


Fig. 3.9. Log_e-transformed leaf number of individual ramets of 6 species of focal plants, in plots sprayed with and without above-ground insecticide during the summer of 2002. Results are shown from a) May 25th, b) June 26th, and c) August 12th. Error bars indicate 95% confidence intervals.

Appendix 1

In order to test for phytotoxic or fertilization effects of the insecticide treatments on plants themselves, I conducted a growth chamber experiment during the summer of 2001 using as model species the forb *Achillea millefolium* L., and the grass *Festuca hallii* Piper. The experiment followed plant growth from the seedling stage until most plants had begun to produce new ramets from the original genet (5 weeks from seedling to harvest). In order to keep the roots intact for root biomass measurement the plants were grown in a 3:1 sand: potting soil mixture in pots with a diameter of 6.5 cm. The insecticides Lorsban 4E and Lorsban 15G were applied at field application rates beginning when the seedlings were 14 days old (June 29th). Plants were arranged in a randomized block design with 1 seedling per pot, and 1 treatment per species (control above-ground insecticide, below-ground insecticide, both), with 15 replicates. Since there is considerable variation in light levels within the growth chamber (M. Brown, pers. comm.), the blocks were repositioned to a randomly chosen location on the growth chamber shelf after each set of measurements to reduce between-block variation.

At the end of the experiment all plants were harvested and dried at 70 °C. Root and shoot biomass measurements were taken on each individual. Plants that died during the experiment (2 of 60 *Festuca hallii*) were mistaken as *Festuca hallii* due to seed contamination (2 plants) or pots where 2 seedlings had been mistaken for one (again, 2 *Festuca hallii*) were not included in statistical analyses.

Analyses were conducted using PROC MIXED in SAS 8.2, as described in the Methods section. Again, random effects were removed from the model until the reduction in the goodness of fit of the entire model was statistically significant. There were no separate or interactive effects of any insecticide treatment on shoot or root biomass (Table 3.13). This finding does not disprove direct effects of the insecticides on plant growth, but it is not supportive of such effects as a direct mechanism for the patterns seen in this study.

Table 3.13. Effects of above- and below-ground insecticide treatments on shoot and root biomass of 2 common rough fescue prairie plants from a growth chamber experiment with no insects present.

Species	Biomass measure	Above-ground insecticide effect		Below-ground insecticide effect		Above*below-ground interaction		Random effects retained	
		F	P	F	P	F	P		
<i>Achillea millefolium</i>	shoots	$F_{1,28} = 3.10$	0.0890	$F_{1,28} = 0.11$	0.7453	$F_{1,28} = 0.53$	0.4718	BGI*block	
	roots	$F_{1,28} = 0.84$	0.3669	$F_{1,28} = 0.22$	0.6477	$F_{1,23} = 1.14$	0.2953	BGI*block	
<i>Festuca hallii</i>	shoots	$F_{1,28} = 1.17$	0.2883	$F_{1,28} = 3.74$	0.0654	$F_{1,28} = 2.08$	0.1624	AGI*block	
	roots	$F_{1,37} = 0.35$	0.5560	$F_{1,37} = 3.61$	0.0654	$F_{1,37} = 0.01$	0.9398	Block	

CHAPTER 4

CHEMICAL MANIPULATION OF THE BELOW-GROUND ARTHROPODS OF NATIVE ROUGH FESCUE PRAIRIE AND THEIR ECOLOGICAL ROLES IN THE PLANT COMMUNITY

Introduction

Below-ground arthropods in herbaceous communities are responsible for a substantial component of arthropod herbivory (White and French, 1968; Brown and Gange, 1992; Maron and Jefferies, 1999). The arthropods most often implicated in this damage are the root-chewing larvae of crane flies (White and French, 1968; Blackshaw, 1984), scarabeid beetles (Ueckert, 1979; Coffin et al., 1998) and elaterid beetles (Cockbill et al., 1944; Brown and Gange, 1992). In early successional environments herbivory by these taxa has been shown to reduce species richness directly by killing seedlings (Brown and Gange, 1989a). Species-specific root herbivory may also change the outcome of interspecific competition by reducing growth rate (Notzold et al., 1998), altering root architecture (Ramsell et al., 1993), or increasing nitrogen transfer between plants (Murray and Hatch, 1994). Such direct and indirect mechanisms may scale up to shifts in plant community structure (Ganade and Brown, 1997) although more complex faunally mediated interactions may do the same (Gibson et al., 1990).

Despite these findings, our understanding of the importance of below-ground insect herbivory to plant communities remains limited (Blossey and Hunt-Joshi, 2003). Experimental evidence for significant effects of below-ground

insect herbivory on plant community structure comes mostly from early successional communities (Brown and Gange, 1989b; 1992). In mature communities, most observations of the effects of below-ground insects on community structure are during outbreaks (Ueckert, 1979; Coffin et al., 1998; Maron and Jefferies, 1999; but see Gibson et al., 1990). However, insect outbreaks are not the norm in natural plant communities (Faeth, 1987), and below-ground insect outbreaks tend to occur over a small area (Watts, 1982). Manipulation of insect numbers at non-outbreak levels, to examine resulting changes in the plant community, would provide ecologists with greater generality in their conclusions regarding the importance of below-ground insect herbivory to plant community structure. The value of such studies will be greater if they are accompanied by surveys of soil insect density and species composition. Such surveys will allow investigators to advance further hypotheses regarding the specific plant-insect or faunal interactions involved. Additionally, it will allow them to assess more realistically the likelihood that soil insects have any effect on plant community structure, independent of the results of manipulation.

The primary objective of my research program was to determine how arthropods affect the basic measures by which plant communities are described, such as diversity, plant species composition, and primary production. I conducted a two year manipulative experiment of the above- and below-ground arthropods in a native grassland community, taking regular measurements of plant response. I also surveyed the soil arthropod fauna. Here I describe the soil arthropod taxonomic composition, and review the feeding habits of the individual taxa as

described by other researchers. I then present the results of the insecticidal treatments used to control them. Finally, I compare the densities of the dominant soil insect herbivores during this study with densities found at sites where significant impact (most often outbreak level) was observed in other studies. This approach was used to determine whether our site had soil insect densities shown to affect plant community structure in similar community types.

Methods

Study site

This study was conducted from May 2001- October 2002 at Kinsella Beef Cattle Research Ranch, a 3200 ha ranch north of Kinsella, in Beaver County, Alberta. It is located in the aspen parkland ecoregion, which is typified by an undulating morainal landscape. The site itself (53.092° N, 111.552° W) is a self-sown grassland that has never been ploughed or tilled. It consists of two adjacent fields with a total area of 20 ha, and a gentle, south-facing slope, bounded and separated by barb-wire fencing to exclude cattle. Both fields contain, and are bordered to the north, by clonal stands of aspen (*Populus tremuloides*). Most phytomass is below-ground (87%). The soil is Elnora, a thin, well drained black chernozem typical of grasslands in the Viking Upland of Beaver County (Howitt, 1988). Both fields have been grazed each fall by cattle for 20 years, but cattle were excluded for the duration of the study.

The climate in this region is continental; 5 months of the year (Nov-Mar) have average daily temperatures below 0°C (Environment Canada), and most

plant growth occurs between early May and late August (B. Irving, pers. comm.). 2001 and 2002 were unusually dry years. Precipitation during the growing season of 2001 and the prior winter was 186.6 mm, 56% below the 37 year average of 428 mm. Precipitation during the growing season of 2002 and the prior winter was 183.3 mm, 57% below the 37 year average of 428 mm (Fig. 4.1). Annual precipitation in these successive years was the lowest of the previous ten years for which data were available.

Experimental design

In order to minimize vegetational heterogeneity within and between study blocks, the areas chosen were free of aspen, had little or no wolf willow, and were at least 5 m from any disused roads or fences. In order to examine effects of above- and below-ground arthropods, I employed a complete randomized block design with 4 treatments: Control (no insecticide), above-ground insecticide, below-ground insecticide, and both (above- and below-ground insecticides), with 10 replicates. Each block had dimensions of 15 x 19 m, with the 19 m sides running roughly east-west. Each treatment plot had an area of 6 x 8 m. A 1 m wide mowed buffer was made around the plots and between them. In order to reduce edge effects (disturbance by other researchers, invasion of insects from the surrounding community), all sampling was conducted in the inner 4 x 6 m of each plot. Blocks were separated by a minimum of 25 m and a maximum of 200 m.

Chlorpyrifos is the active ingredient of both insecticides employed. It is a broad spectrum insecticide (Kenaga et al., 1965) whose mode of action is

cholinesterase inhibition (Eto, 1974). The below-ground insecticidal treatment was Lorsban 15G (Dow Chemicals; 15% active ingredient) a granular insecticide mixture. Each treated plot received 64g of insecticide in 670g of sand, at the rate recommended for control of white grubs in turfgrass (Johnson, 1998). It was released from a 1L plastic jar, strapped to a 1.5m plastic broomstick, by sweeping this device in a wide (~2m), lateral arc, making 4 passes per plot, moving from the west to the east end of the plot. It was applied on May 10th 2001, July 11th 2001, May 3rd 2002, July 3rd 2002, and August 14th, 2002.

The above-ground insecticide mixture was Lorsban 4E (Dow Chemicals; 48% active ingredient), sprayed in a water emulsion at a concentration of 2.8 mL/L, from a backpack sprayer with a 15 L capacity. In each spraying event, all plots treated with above-ground insecticide received 4.2 mL of Lorsban 4E in 1.44 L of water. This concentration is recommended for control of adult grasshoppers in cereal crops (Johnson 1998), and it was very effective in reducing numbers of the major above-ground insect orders, and the frequency and intensity of plant damage (Chapter 3). Control plots, and plots treated with the below-ground insecticide alone, received the same volume of water. I sprayed the plots every 2 weeks, from early May until late August of both years. The response of the plant community to these treatments was measured in terms of plant canopy cover and standing crop during both seasons. These results are reported elsewhere (see Chapter 3).

Below-ground insect sampling

Below-ground macroarthropods were collected by hand from soil cores. Cores were removed from the center of 1m x 10cm subquadrats of vegetation sampled for above-ground biomass. Each had a diameter of 16 cm and a depth of 10 cm (an area of 0.02 m²). A narrow shovel with a tapering concave blade (12-14 cm width) was used to cut vertical sides of the core and then remove it from the ground. I located macroarthropods visually by breaking apart the core, tearing apart the roots, and sifting the soil through copper sieves of progressively smaller pore diameters with a smallest pore diameter of 2 mm. In preliminary trials, I sifted the soil through smaller pore diameters (1.5 mm and 1 mm) but rarely found any more macroarthropods. Captured invertebrates were stored in plastic scintillation vials in 70% ethanol. I collected two cores per plot on May 4th, 2001 (pre-treatment) and May 15th 2002, and one core per plot on July 9th, and August 23rd 2001. When two cores were collected per plot I pooled insect counts within plots and divided counts by two to correct for greater sampling area in analysis and display of data.

Soil microarthropods were collected from smaller cores taken adjacent to the macroarthropod cores. These cores were 4.75 cm in diameter and 15cm deep, and were made by pounding a section of PVC into the soil. I removed these samples after removing the larger soil core. They were stored in Zip-Loc bags and the microarthropods were collected using a modified version of a Kempson extractor (Southwood and Henderson, 2000). The extractor had a foil-covered wood frame with 3, 60 W incandescent bulbs which maintained internal

temperature of 50°C. All PVC cores were inserted into 5 cm diameter holes in a horizontal plywood sheet that was positioned beneath the bulbs. Prior to being mounted in the frame, the soil surface in the cores was wetted with 10 mL water, and the tubes were sealed at the soil-surface end with 1.5 mm plastic garden netting attached with a rubber band, then inverted such that the soil surface faced down towards the preservative fluid (brine with detergent in beer cups). This design is similar to one used in a recent arthropod survey of boreal forest soils (C. Buddle, pers. comm.). I collected Kempson cores on all dates when macroarthropods were sampled, and on August 14th 2002.

The extractor was kept running until the soil cores had contracted in the tubes from water loss (3-5 days). A researcher who has conducted many previous studies of grassland microarthropods, believes that this method probably had a collection efficiency of about 70% (D. Kanashiro, pers. comm.) but I did not evaluate its efficiency directly. All specimens were stored in 70% ethyl alcohol. The mites and other microarthropods were separated from soil and other debris in a petri dish with a 1 cm grid, searched with a dissecting scope set at 25 x.

Insect identification

Insects were identified to varying levels of taxonomic resolution, depending upon the resources available and their frequency within the samples. With the exception of ants, most soil insects were in the larval or pupal stage. All insects were identified to order using standard entomological texts (Stehr, 1991; Borror et al., 1992). Ants were identified to the subfamily using Bolton (1994)

and to species using Wheeler and Wheeler (1963). Assistance with identification was provided by various experts for each taxonomic group (see Acknowledgements). With the exception of ants, species or genus level identification of macroarthropods was performed on a subset of individuals considered part of the same morphospecies as assessed by careful observation. Therefore, the taxonomic list is not complete, but it is an accurate assessment of the numerically dominant arthropod taxa. Likewise, not all mites were examined in detail; 113 mites from 5 randomly chosen samples were identified by an acarologist. Information on the feeding habits of the numerically dominant soil arthropods was derived from several sources (references in Table 4.1; H. Proctor, pers. comm.).

Statistical Analysis

In order to assess effects of the insecticidal treatments on mite counts, I used mixed model analysis of variance, with each treatment as a fixed factor and block as a random factor (Littell et al., 1996) for each harvest. In order to examine variation in insecticide effectiveness between harvests, I also conducted a single mixed model analysis of variance with collection date as a third fixed factor. I used the PROC MIXED procedure in SAS 8.2 (SAS Institute 2000) for the above analysis, with the successive removal of non-significant random effects from the model, as used in analysis of plant community effects (see Chapter 3).

Due to low insect density and patchy occurrence, it was immediately apparent that macroarthropod count data for each date were not amenable to

statistical inference. In order to increase the power of these statistical tests, all post-treatment macroarthropod counts were summed to provide a cumulative count per plot. This dataset allows me to evaluate the effectiveness of the insecticide treatments, though not the particular dates when they were most effective. The baseline (pre-treatment) insect harvest data were analyzed separately. Because the granular insecticide is promoted as a control for macroarthropod larvae (Johnson, 1998), larval counts were analyzed separately from counts of ants and other adult arthropods. Ant counts were also analyzed separately from other adult macroarthropods, since the latter tended to be epigeic (i.e. not true "soil" insects at time of capture), so might be affected differently from the ants, which were found in subterranean colonies.

Macroarthropod count data were not normally distributed for any of the above groups. Visual inspection of the graphs for larvae, ants, and adults indicated that the data fit best to a Poisson distribution. Therefore, the effects of the insecticides on soil macroarthropod counts were analyzed using generalized linear mixed models for Poisson data with a log transformation (using the %GLIMMIX macro; Littell et al., 1996). Insect count was the dependent variable, the insecticide treatments were fixed factors, and block was a random factor.

Soil insect density: literature survey

In order to determine if soil insect densities were at levels with the known potential to affect plant community structure, I conducted literature searches for

studies in which the dominant soil insect taxa at my site had significantly affected other plant communities. These insects included most of the common agricultural pests in annual crops and pasture (Cockbill et al., 1944; Watts, 1982).

Congenerics, or root-feeders in the same family, also using graminoid-dominated habitats, were considered comparable with insects found at my site. For each taxon, I present mean outbreak densities (larvae/m²) from each study and densities from my own data during 2001 and 2002, along with a description of the plant community. When non-outbreak densities are available in the same study, I include them, with the caveat that insect impact at non-outbreak densities was not determined experimentally.

Results

Soil arthropod fauna

The soil insect fauna included ants, coleopteran and dipteran larvae, some root aphids, and adult carabid and staphylinid beetles (Table 4.1). Ants (Formicidae) were the numerically dominant soil macroarthropods (Fig. 4.2). Of the other macroarthropods, the numerically dominant groups were (in order) various life stages of the elaterid *Ctenicera destructor* Brown, root aphids (Aphididae: Fordini), assorted fly larvae, small (~5 mm length) adult carabids, various life stages of a scarabeid of the genus *Phyllophaga*, assorted lepidopteran larvae, adult staphilinids, and tipulid larvae. Root aphids were rare in the samples and not found in the first year, but their abundance was probably underestimated by our visual searches, since those located were very small (~1 mm length),

immobile, and unpigmented. Evidence for this hypothesis is provided by an arthropod survey in which root homopterans were found in abundance at this site using different extraction methods (Birkigt, unpublished). Root aphids were usually found with *Acanthomyops claviger* Roger (Mayr), an obligate root aphid tending ant. The other ants are omnivorous, feeding both on insect larvae and on the honeydew secreted by root aphids. The known coleopteran and dipteran larvae are root and seed feeders (Table 4.1).

Mites (Acari) were the numerically dominant soil microarthropods (Table 4.2). The mite samples examined in more detail were dominated by the suborders Oribatida and Prostigmata, with some individuals from the suborders Mesostigmata and Astigmata. They occupy most trophic positions in the soil food web (including herbivores), but most specimens were fungivores or predators of nematodes and other microarthropods.

Effects of insecticide treatments on soil insect numbers

Soil mite counts were reduced by the below-ground insecticide in May 2002 (Fig. 4.3, Table 4.3) but were never significantly affected by the above-ground insecticide. There were also trends towards a reduction in mite numbers by the below-ground insecticide on 2 of the 3 other sampling dates (Fig. 4.3). In contrast to the response of mites, cumulative counts of dipteran, coleopteran, and lepidopteran soil larvae were significantly reduced by the above-ground insecticide, but not by the below-ground insecticide (Fig. 4.4, Table 4.4). Cumulative counts of adult insects (less the ants) were not affected by either

treatment, though the effect of the below-ground insecticide approached significance (Fig. 4.4, Table 4.4). No insecticide treatment significantly reduced ant counts (Fig. 4.4, Table 4.4). No measures of plant community structure or function were affected by the soil insecticide treatment but the above-ground insecticide caused an increase in plant cover in the second year of application (see Chapter 3).

Comparison of my insect densities with outbreak levels

I located 7 studies which recorded density of soil insects common at my site and related them to plant damage (Table 4.5). Damage had been assessed by various measures of the whole plant community, such as reduced cover (Ueckert, 1979), biomass (Blackshaw, 1984), and agricultural yield (Cockbill et al., 1944), and changes in plant species composition (Brown and Gange, 1992). Counts of the dominant below-ground insect herbivores at my study site were always considerably lower than those for the same taxa at outbreak levels in other natural and agricultural communities; even *Phyllophaga* scarabeids, considered an important pest in native North American grassland (Watts, 1982), were never at densities greater than 1/6th of outbreak levels, and in the second year of study, their densities were well below the *non-outbreak* levels in a similar system (Lura and Nyren, 1992).

Discussion

The below-ground insect herbivores: ecological importance

With reference to the previous literature, counts of all soil insect herbivores were well below outbreak levels for those taxa in other systems. This finding suggests that in this system, below-ground insect herbivory by these taxa is unimportant to plant community structure and function. If so, this is in strong contrast with the early successional systems where below-ground insect herbivory has well-demonstrated effects on cover and community composition (Brown and Gange, 1992). Mortimer et al. (1999) suggest that late successional plant communities are likely to have higher densities and diversity of soil macroarthropods than early successional communities, but they are also likely to have been colonized by their pathogens. Furthermore, mature, perennial plants are better able to compensate for below-ground insect herbivore damage (D'Arcy Burt and Blackshaw, 1991; Crutchfield and Potter, 1995), suggesting that, independent of density, below-ground insect herbivory in this system will impact the plants less.

It could be argued that this site has certain special properties that defy comparison with the other community types listed. This is the first study to examine impacts of below-ground insect herbivory during drought. The negative effects of below-ground herbivory on plant growth are usually exacerbated by water stress (Blossey and Hunt-Joshi, 2003). However, the control plot densities of all groups considered of agricultural importance were lower during the second year of the drought (Table 4.2). This is compatible with findings of increased

larval mortality of below-ground larval insect herbivores in conditions of water stress (Potter and Gordon, 1984) and behavioural strategies to avoid low moisture conditions (Zacharuk, 1962). Further investigation of the opposing roles of soil insect mortality or aestivation, and plant stress, in determining the effects of below-ground insect herbivory on plant growth in drought-prone systems is clearly warranted.

The role of ants

The abundance of ants that tend root aphids suggests that extensive herbivory by homopterans occurs in this system, a form of herbivory that has been not been examined by other workers, who have concentrated on below-ground herbivory by insects of known agricultural importance (Blossey and Hunt-Joshi, 2003). Whether these ants have net positive or negative effects on plant growth is perhaps the most interesting question that remains to be answered regarding plant-insect interactions in this system. Due to their dual role as protectors of homopterans from predation (Way, 1963; Takada and Hashimoto, 1985), and predators of other insects (Holldobler and Wilson, 1991), ants on above-ground plant parts may improve measures of plant performance (Messina, 1981; Karhu, 1998; Sipura, 2002) or worsen them (Adlung, 1966; Rico-Gray and Castro, 1996; Sipura, 2002). The abundance of obligate and facultative aphid-tending ants (Wheeler and Wheeler, 1963; Holldobler and Wilson, 1990), and their co-occurrence with root aphids, suggests that similar processes may be at work in the root - root aphid - ant system. However, in a recent review of ant-plant

interactions, Beattie and Hughes (2002), stated that no studies have examined the effect of this association on plants. I attribute this in part to the predominance of early-successional communities in studies that have addressed the community-level effects of below-ground insect herbivory. Since root aphids depend upon ants to reach their food source, root aphid herbivory cannot occur until subterranean ants have established colonies, most likely late in succession (Mortimer et al., 1999).

I suggest that any negative effect on plant growth due to ant tending of root aphids is buffered by the omnivorous diets of 3 of the 4 most abundant ants (*Lasius neoniger* Emery (Gregg), *L. sitkaensis* Pergande (Wilson), and *Myrmica lobicornis fracticornis* Emery; Wheeler and Wheeler 1963). Ants of the genus *Lasius* are known to feed on the eggs of root-feeding scarabeids and the larvae and eggs of other insect root herbivores (Lopez and Potter, 2000; Zenger and Gibb, 2001), and the red wood ant *Formica rufa* can substantially suppress populations of soil-dwelling elaterid larvae (Adlung, 1966). During this study, I also observed *Lasius* ants attacking and carrying above-ground lepidopteran larvae adjacent to the study plots.

Insecticide effectiveness

The ineffectiveness of the soil insecticide is a disappointing result with respect to measuring the separate effects of above- and below-ground insects on plant growth in this system. I suggest that this occurred as a result of the exceedingly low rainfall. Brown and Gange (1989b) noted that granular

chlorpyrifos becomes active in the soil once it is washed in by rain. Artificial watering is encouraged when using granular chlorpyrifos on lawns (Johnson, 1998). In the future, we will use smaller plots and water them after insecticide application; this method was not tractable at the spatial scale of the original study plots. This result illustrates the importance of measuring true effects on soil fauna during attempts to manipulate their numbers for studies of plant community effects. This result also has an important implication for any investigation of the interaction between drought and below-ground insect herbivory: if one wishes to address this issue using granular insecticides, it would be unadvisable to consider the drought treatments to be ambient water levels, as this could lead to an artifactual result, in which a treatment with water and the granular insecticide would be effective, and a treatment with the insecticide but without water would not.

Summary of results

These results suggest that the insects generally implicated as the most important below-ground insect herbivores in other natural and agricultural systems, were not important to the structure of this plant community during the period of study. In this rough fescue prairie community the most abundant soil macroarthropods are ants, which have the potential to both suppress insect herbivore numbers, and promote herbivory by root-feeding homopterans. A fruitful program of further research would be an examination of interactions

between drought and importance of below-ground insects at non-outbreak levels, and the role of ants in promoting or suppressing plant growth.

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Table 4.1. Results of a survey of the soil insects of two mixed-grass prairie fields at Kinsella, Alberta, during the summers of 2001 and 2002. These are the numerically dominant soil insects with information on their diet and species richness (at the site) when available.

Taxon	Species	Diet
Homoptera: Aphididae: Fordini	1	Root sap feeder ¹
Coleoptera: Scarabaeidae: <i>Phyllophaga</i> sp.	1	Root chewer ^{1,2}
Coleoptera: Elateridae: <i>Ctenicera destructor</i>	1	Roots and seeds ³
Coleoptera: Carabidae	6	Other insects, and spiders ¹
Diptera	4	Varied ¹
Diptera: Tipulidae	1	Root chewer or saprovore ^{1,2}
Lepidoptera	4	Living plant matter ¹
Hymenoptera: Formicidae: <i>Tapinoma sessile</i>	1	Tends root aphids, scavenges for plant honeydew ⁴
Hymenoptera: Formicidae: <i>Myrmica lobicornis fraticornis</i>	1	Plant honeydew, other arthropods ⁴
Hymenoptera: Formicidae: <i>Lasius</i> sp.	2	Tend root aphids, forage for living and dead insects ^{4,5}
Hymenoptera: Formicidae: <i>Acanthomyops claviger</i>	1	Tends root aphids, likely in an obligatory mutualism ^{4,6}

¹Borror et al., 1991

²Watts et al., 1982

³Zacharuk 1962

⁴Wheeler and Wheeler 1963

⁵Traniello 1983

⁶Holldobler and Wilson 1990

Table 4.2. Diversity and relative abundance of mites (Acari) in two mixed-grass prairie fields at Kinsella, Alberta during the summers of 2001 and 2002. These are the numerically dominant taxa in 5 samples with a total of 113 mites randomly chosen from 5 harvests with information on their diet when available (H. Proctor, pers. comm.).

Taxonomic levels	Specimens	Diet
Suborder Mesostigmata		
Cohort unknown	3	microarthropods, nematodes
Cohort Dermanyssina		
Superfamily Ascoidea		
Family Ascidae		
<i>Asca</i> sp.	1	nematodes
<i>Gamasellodes</i> sp.	4	microarthropods, nematodes
Family Phytoseiidae	1	microarthropods, nematodes
Superfamily Dermanyssoidea		
Family Laelapidae	4	microarthropods, nematodes
Suborder Prostigmata		
Cohort Eupodina		
Family Cunaxidae	2	microarthropods
Superfamily Eriophyoidea	1	live plants
Superfamily Erythraeoidea		
Family Erythraeidae	1	microarthropods
Superfamily Eupodoidea		
Family Eupodidae	2	fungus
Cohort Heterostigmata		
Family Microdispidae	3	fungus, bacteria
Family Scutacaridae	7	fungus, bacteria
Family Stigmaeidae	1	microarthropods
Family Tarsonemidae	9	fungus, bacteria, sometimes live plants
Cohort Raphignathina		
Family unknown	1	microarthropods
Superfamily Tetranychoidae		
Family Tetranychidae		
Subfamily Bryobiinae	7	live plants
Cohort Eupodina		
Family Tydeidae		
Genus unknown	17	fungus, sometimes predatory
<i>Lorryia</i> sp.	2	fungus, sometimes predatory
Suborder Astigmata		
Family Acaridae	1	fungus, detritus
Suborder Oribatida		
Superfamily unknown	23	fungus, detritus

Superfamily Anderemaeoidea	1	fungus, detritus
Superfamily Eratyctoidea	1	fungus, detritus
Superfamily Eremaoidea		
Family Eremacidae	1	fungus, detritus
Superfamily Galumnoidea		
Family Galumnidae	7	fungus, detritus
Superfamily Oripodoidea		
Family Haplozetidae	3	fungus, detritus
Family Oribatulidae	3	fungus, detritus
Family Oppiidae		
<i>Oppiella nova</i>	1	fungus, detritus
Superfamily Tectocephoidea		
Family Tectocephidae	6	fungus, detritus

Table 4.3. Results of mixed-model ANOVA analyzing effects of two insecticides on mite counts. The full model was run with the random effect (block) and all random effect interactions. Random effects were removed from the model until the difference between the residual log likelihood of the full model and that of the simplified model was greater than 2.6, the critical value at $P=0.01$ with $df=1$. "3-way interaction" refers to the random effect interaction between the above-ground treatment, the below-ground treatment, and block. The second analysis pools all the data and includes collection date as a third fixed factor.

Harvest	Above-ground insecticide effect			Below-ground insecticide effect			Above*below-ground interaction			Random effects retained
	F	P		F	P		F	P		
May 5th, 2001 (pre-treatment)	$F_{1,35} = 1.37$	0.2500		$F_{1,35} = 0.09$	0.7640		$F_{1,35} = 0.18$	0.6736	3-way interaction	
July 3rd, 2001	$F_{1,18} = 0.20$	0.6638		$F_{1,18} = 1.41$	0.2510		$F_{1,18} = 0.53$	0.4775	BGI*block, 3-way interaction	
August 23rd, 2001	$F_{1,36} = 0.18$	0.6724		$F_{1,36} = 0.20$	0.6581		$F_{1,36} = 1.39$	0.2458	AGI*block	
May 15 th , 2002	$F_{1,18} = 0.65$	0.4315		$F_{1,18} = 18$	0.0005		$F_{1,18} = 0.38$	0.5466	AGI*block, 3-way interaction	
August 23rd, 2002	$F_{1,36} = 0.08$	0.7802		$F_{1,36} = 0.41$	0.5237		$F_{1,36} = 1.01$	0.3207	3-way interaction	
All harvests AGI	Num df 1	Den df 89		F 0.01	P 0.9047					

BGI	1	89	1.64	0.2306
AGI*BGI	1	89	0.94	0.3350
Time	4	89	5.61	0.0004
AGI*time	4	89	0.62	0.6500
BGI*time	4	89	1.07	0.3783
3-way interaction	4	89	1.15	0.3406

Table 4.4. Results of mixed-model analyses of variance analyzing effects of two insecticides on cumulative soil insect counts during the summers of 2001 and 2002. Significant results are shown in bold.

Insect grouping	Above-ground insecticide effect		Below-ground insecticide effect		Above-below-ground Interaction	
	F _{1,35}	P	F _{1,35}	P	F _{1,35}	P
dipteran, coleopteran, and lepidopteran larvae	6.25	0.0172	0.85	0.3623	0.21	0.6510
Adult insects except for ants	1.35	0.2533	3.63	0.0650	1.35	0.2533
Ants	0.01	0.9399	0.84	0.3647	2.36	0.1335

Table 4.5. Comparison of soil insect "pest" densities at the rough fescue prairie site with densities of similar taxa in other graminoid-dominated systems, where damage of the vegetation by that insect was observed. As damage was measured using different methods, and not always reported quantitatively, I have not attempted to make quantitative comparisons of damage at these sites with damage at the rough fescue prairie site.

Insect	Data source	Community type	Density (individuals/m ²)	Damage
Elaterid larvae	Cockbill et al., 1945	spring wheat	310	moderate
	Cockbill et al., 1945	spring wheat	440	severe
	Cockbill et al., 1945	spring wheat	500	severe
	My data: May 2001	rough fescue prairie	23.3	little or none
	My data: May 2002	rough fescue prairie	19.8	little or none
Scarabeid larvae	Ueckert 1979	shortgrass prairie	46.3	severe
	Lura and Nyren 1992	mixed-grass prairie	47	severe
	Lura and Nyren 1992	mixed-grass prairie	1.6	reference site
	Wiener and Capinera 1980	shortgrass prairie	280.1	severe
	Wiener and Capinera 1980	shortgrass prairie	25.5	reference site
	My data: May 2001	rough fescue prairie	8.5	little or none
	My data: May 2002	rough fescue prairie	0.9	little or none
Tipulid larvae	Blackshaw 1984	ryegrass pasture	31.5	moderate
	Newbold 1981	ryegrass pasture	202	moderate
	Newbold 1981	ryegrass pasture	164	moderate
	My data: May 2001	rough fescue prairie	9.2	little or none
	My data: May 2002	rough fescue prairie	5.7	little or none
all three taxa	Brown and Gange 1992	mid-successional grassland	1470	moderate
	My data: May 2001	rough fescue prairie	41	little or none
	My data: May 2002	rough fescue prairie	26.4	little or none

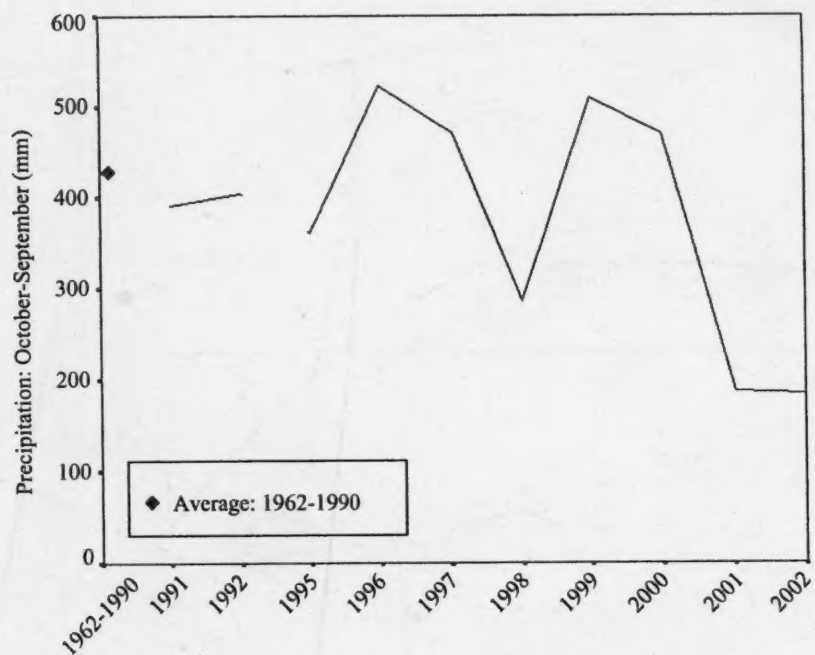


Fig. 4.1. Precipitation records from October to September at Kinsella townsite: 1962-2002. Note that years 1962-1990 are presented as a single average value, and data are missing for 1993 and 1994.

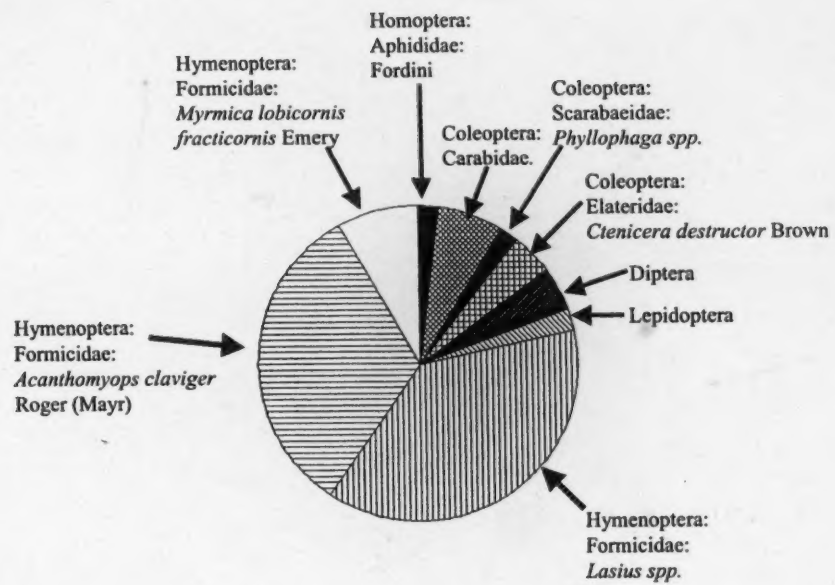


Fig. 4.2. Relative abundance of the 9 most abundant soil insect taxa, from cumulative count data (n=1110 insects total).

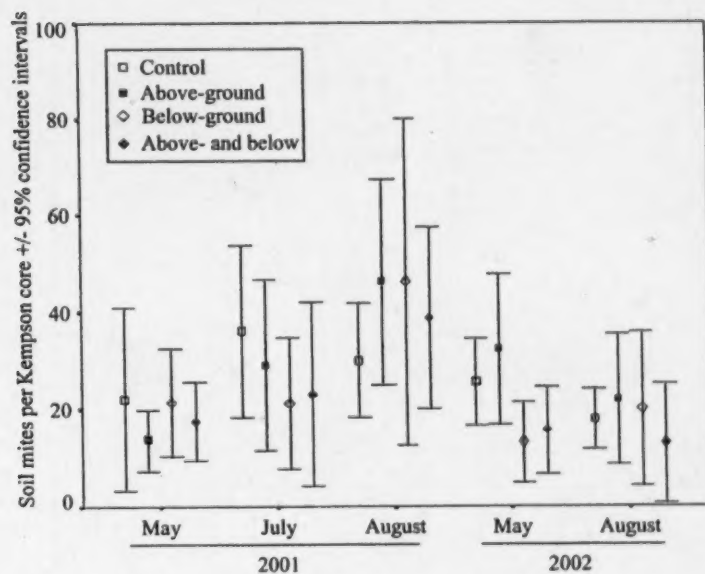


Fig. 4.3. Comparison of mean ($\pm$ 95% confidence intervals) mite counts in the 4 insecticide treatments during the summers of 2001 and 2002.

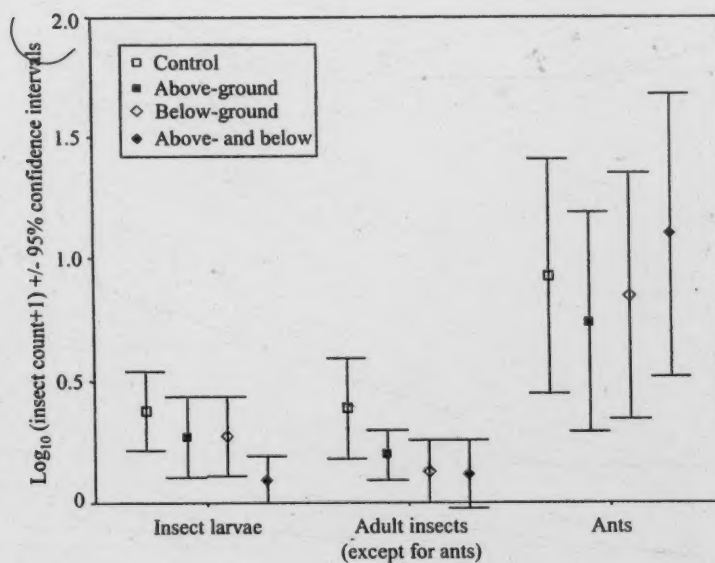


Fig. 4.4. Comparison of $\log_{10}$ transformed mean ($\pm$ 95% confidence intervals) cumulative macroarthropod counts in the 4 insecticide -treatments during the summers of 2001 and 2002.

CHAPTER 5

CONCLUSIONS AND SUGGESTIONS FOR FUTURE RESEARCH

General context

In this thesis I have examined the impact of insects upon primary production and community structure in herbaceous communities. It is placed in the context of two ideas, the first that predators maintain herbivore numbers below levels at which they can substantially affect plant communities (Hairston et al., 1961; Strong et al., 1984), and the second, that herbivores affect plants little because plants are well defended and of low food quality (McNeill and Southwood, 1979; Hartley and Jones, 1997). Thus herbivores, especially insect herbivores (Crawley, 1989) are thought to have little direct effect on primary production or community structure. Cases of successful biological control (Huffaker and Kennett, 1959; de Bach, 1991) are actually seen as evidence for processes that keep insect herbivores "in check" in systems containing insect herbivores along with their prey species. In dissent are researchers who have argued that the evidence shows otherwise (Brown and Gange, 1992; Carson and Root, 2000). I have examined these ideas, drawing data from studies where effects of insects on herbaceous plant communities are measured by chemical suppression, and from an examination of the impact of insect suppression on plant community structure, diversity, and primary production in native grassland.

Data chapter summaries

In Chapter 2, I examined the effects of insects on primary production in temperate herbaceous communities in a meta-analysis, and addressed some long-standing theories of the role of plant community properties in determining the effects of insects upon them. Oksanen et al. (1981) proposed that the relative strengths of "top-down" and "bottom-up" forces in regulating herbivore populations should vary as a function of productivity, as herbivore, and predator, food supply and increases with greater plant production. They asserted that this model was unlikely to apply to arthropods, but later conceded that the data to test this hypothesis were lacking (Oksanen and Oksanen, 2000). Root (1973) proposed that agricultural systems with greater diversity were less prone to yield losses from specialist insect herbivores. Although the analogy has often been made to natural communities (particularly forests) no one had examined the relationship between the effects of insects on primary production and plant species diversity. I addressed these hypotheses using data from studies in which the authors had applied insecticide to a self-sown natural community, and examined the effects of insect herbivory on primary production.

There was a significant increase in primary production as a result of insect suppression, suggesting that herbivory is the dominant mechanism through which insects affect plant communities. However, effect size was not related to productivity, supporting the view that the ecosystems exploitation model is only applicable to vertebrates (Oksanen et al., 1981). If this is the case, then the relationship between productivity and top-down control of primary production

may be a weak one, given that the effects of invertebrate herbivores on plant biomass are quantitatively similar to the effects of vertebrates (Bigger and Marvier, 1998). Additionally, effect size was not correlated with plant species richness. I conclude that although insects lower primary production in a diversity of temperate herbaceous communities, the basic measures by which such communities are often described have little effect on the proportional impact insects have upon primary production.

In Chapter 3, I describe the impacts of insects on community function, structure, and composition in a native grassland of low productivity and high diversity. This study was motivated by the debate between authors who have proposed that insects should have little effect on ecosystem function and plant community structure due to top-down control by predators (Hairston et al., 1960; Strong et al., 1984) or low food quality (McNeill and Southwood, 1979; Hartley and Jones, 1997), and authors who have repeatedly observed significant effects of insect herbivory on primary production (Coupe and Cahill, 2003), community structure (Huffaker and Kennett, 1959, Berdowski and Zeilinga, 1987; Auge et al., pers. comm.) and succession (Brown and Gange, 1992; Bach, 1994; Carson and Root, 1999; 2000). I used above- and below-ground insecticides in a randomized block design, to suppress insect herbivores on both above- and below-ground plant parts, and examine their separate effects over a two year period. The below-ground insecticide was largely ineffective, so the most meaningful conclusions can be drawn from the results of the above-ground insect suppression. I assessed the effects of insect suppression on the plant community

by regular measurements of above and below-ground plant biomass and cover. During the 2002 growing season I also observed focal plants of the 6 most common forb species, to evaluate interspecific differences in herbivory, and the effects of insects on plant growth and mortality. In order to test for shifts in floristic composition, I used a multivariate statistical approach known as the blocked multiple response permutation procedure (MRBP; Zimmerman et al., 1985), and indicator species analyses (Dufrêne and Legendre, 1997). A drought began in 2001 and continued until 2002, exerting substantial negative effects on plant growth. This presented a unique opportunity to examine the impact of insects on plant community structure during a period of extreme plant stress.

During the first year, primary production, root biomass, and cover were unaffected by insect suppression. In 2002, the second year of the drought, there was substantially lower cover and biomass. Again, primary production and root biomass were not affected by insect suppression. However, during July and August 2002, cover was higher in plots sprayed with above-ground insecticide, suggesting that insect herbivory reduced plant cover. Additionally, plant species richness was higher in plots sprayed with above-ground insecticide in August. In the focal plant experiment, insect damage was plant species-specific, with two species experiencing little or no chewing insect damage and 4 species frequently experiencing low levels of damage. However, focal plant growth and survival were rarely affected by insect suppression. The MRBP revealed several differences between treatments in floristic composition. Indicator species analyses revealed several significant but sporadic effects of the treatments on

species-specific biomass and cover, with significant increases in single species biomass in response to above-ground insect suppression.

The species-specificity of insect damage and significant cover and biomass increases of several species in response to above ground insect suppression, and the increased cover in plots without above-ground insects, suggests that insects play a significant, but minor role in affecting community composition. The lower species richness in plots without above-ground insects in 2002 is compatible with the model of Olff and Ritchie (1998) predicting effects of insects on plant community structure in systems of low productivity. They are not compatible with findings where above-ground insect herbivory has increased species richness, attributed to a reduction in the competitive ability of certain species or species groups (Brown and Gange, 1992; Carson and Root, 2000). I suggest that this result can be attributed to an interaction with the drought. Such interactions have been predicted on the basis of improved reproductive performance of grasshoppers in warm, dry weather, and because moderate water stress may improve food quality for some insect herbivores (Mattson and Haack, 1987; Koricheva et al., 1998; Schowalter et al., 1999).

In Chapter 4, I presented a survey of soil arthropods of the study site, along with the effects of the insecticides on soil arthropod numbers. This study was motivated by the emerging belief that below-ground insect herbivory has strong effects on primary production, community structure, and succession (Blossey and Hunt-Joshi, 2003). My goal was to determine density and taxonomic composition of the soil insect fauna in order to infer its possible

importance to the plant community. I collected and identified the soil arthropods, surveyed the literature in search of studies that had found significant effects of those same insects on plant community structure, and then compared density at those sites with density at my own. I also measured the effectiveness of the insecticide treatments on cumulative numbers of epigeic adult insects, ants, and soil insect larvae.

Most of the below-ground insect fauna at this site were typical of native North American grassland, including coleopteran, dipteran, and lepidopteran larvae that are considered pests in agricultural systems and rangeland (Watts et al., 1982). From my literature survey of outbreak densities I suggested that those occurring at my site were at such low densities that they were unlikely to have affected plant community structure. However, ants (Hymenoptera: Formicidae) and aphids (Homoptera: Aphididae) were unexpectedly abundant, with ants comprising the majority of soil macroarthropods. The below-ground insecticide did not reduce counts of soil macroarthropods and suppressing mites only in the second year of application. By contrast, the above-ground insecticide reduced cumulative counts of the below-ground insect larvae that were the target of the below-ground insecticide. These results suggest that caution should be warranted in the interpretation of any study utilizing chemical suppression of fauna, when effects of the manipulation on those fauna are not measured.

Future research

This research program uncovered a number of promising avenues for further study. In the meta-analysis it was found that species diversity is not related to the impact of insects on primary production. This is in contrast to a large body of theory from cropping systems. The cause of this disparity between the importance of diversity in agricultural and natural systems is in need of investigation. It may simply be that agroecologists have used different criteria for evaluating the value of crop diversity (crop yield alone rather than total plant biomass). However, differences between these systems in insect community structure, food quality, and plant spacing, may also be responsible. Manipulative experiments involving crop species assemblages and assemblages of plants present in self-sown communities, with further manipulation of diversity and of spacing, could provide progress in this area. The analysis of the effects of productivity on the impact of insect herbivory would also have benefitted from an independent measure of productivity, which would have allowed the effect size to be plotted on the y axis, providing greater statistical power than in a nonlinear model (Shepperd, 1999).

The focal examination of effects of insect suppression on plant community structure of rough fescue prairie was unique in its examination of effects during drought years. The results are consistent with the hypothesis that drought amplifies the effects of insect herbivory, but in this experiment the severity of drought was confounded by the time that had passed since the experiment had begun. In other words, the observation of a significant effect in this case could

equally be due to the fact that the manipulation had proceeded for a longer time, rather than due to the fact that the manipulation co-occurred with a drought. Factorial experiments in which water availability is manipulated in tandem with manipulation of insect numbers would be a sound test for an interaction between water stress and the impact of herbivory. An alternative would be to conduct separate experiments on different years and test for a relationship between climate and insect herbivory, thus avoiding any confound. A reversal of the effects observed in subsequent years of this study concurrent with changes in precipitation, rather than a continued accumulation of effects, would also support the existence of such a relationship.

The soil insect survey highlighted a topic that will be both a challenge and a boon to any future researcher in grassland community ecology: the role of subterranean ants in grassland community structure. Ants tend root aphids, but they also prey upon the soil insects traditionally considered pests in grasslands. An investigation of their separate roles as facilitators of root aphid herbivory, and predators of these other soil pests, would require methodological breakthroughs in the investigation of the biotic interactions in soil. Such breakthroughs can be made, but only with imagination and patience.

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